SPECIES AND ASSEMBLAGE RESPONSES OF CARABIDAE (COLEOPTERA) TO FOREST HARVESTING: CONTRASTING CLEARCUT AND PATCH RETENTION REMOVALS IN HIGH-ELEVATION FORESTS OF CENTRAL BRITISH COLUMBIA

by

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Executive Summary

During the summer months of 1995 and 1996, carabid beetles were collected with pitfall traps in high elevation forest near Smithers, BC, and used to investigate three research questions: 1. Can standard pitfall trap design and collection fluid be improved for trapping Carabidae in this forest system? 2. Do carabids show assemblage patterns correlating with localized habitat types, therefore allowing the later to be used for designing land use strategies promoting conservation of the fauna? 3. Will a harvesting regime retaining small patches of timber (0.1-2.0 ha) serve as a more effective means of conserving carabid fauna with respect to traditional clearcutting? A modified pitfall trap design with an integrated lid was found to be preferable to a standard, open-topped design for several reasons. The lid restricted entrances of small vertebrates and the accumulation of rainwater, supporting extended trapping regimes by increasing sample preservation. The lid's integral nature made the trap unit convenient to carry, employ, and collect from. An experimental showed that although two carabid species, *Calathus advena* Lec., and *Elaphrus americanus* Dej., were caught in significantly different numbers between designs, results were not consistently higher toward either trap type. No difference was detected in the five other common carabid species. Ethylene glycol was found to be a superior preservative to saturated brine, and there were no differences in carabid species catches between the two. The modified trap/glycol combination was used in larger scale trapping and carabid beetles were found to have only a "loose" association toward localized habitat classifications known as "site series". Few species differences were evident between four commonly occurring site series classifications.

However, assemblage patterns evident *via* cluster analysis were consistent between years, and showed that the 09 site series was faunistically distinct. Site series was used to ensure replication of habitat sampling for comparisons of clearcut and patch retention harvesting types. Twenty-eight species were collected with 92.4 % of the catch in four species. Plots comparing mature forest with edge, patch and harvested areas showed that the majority of species did not fit previously reported classifications with respect to response to disturbance. A new suite of classifications is proposed, correlating response patterns with degree of disturbance in treatments. For example, species previously reported as mature forest specialists were found to occur commonly, but less abundantly, in open habitat. Several explanations are offered for this trend, the most promising being in the context of an absent fauna, specialized to colonizing cleared habitat. This occurred specifically for the genera *Amara* Bonelli and *Harpalus* Latreille, but may represent a more general phenomenon where colonizing specialists had not reached the study site and hence were not competing with resident forest species for cleared habitat. This hypothesis is proposed with the observation that the study landscape had only minor levels of harvesting. Patch retention harvesting, when compared with clearcutting, harboured a fauna more similar to undisturbed forest. However, it was noted that the creation of small patches without a concurrent reduction in harvest volume would sacrifice mature forest habitat, essentially increasing "edge" effects. In such instances patch retention may be an undesirable harvesting strategy.

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Introduction: Beetles, Forests and Biological Diversity

The case for conservation of forested habitats has been made loud and clear, especially in the tropics (Sutton *et al.* 1983) but also recently for many temperate biomes (Okland 1995; Winchester and Ring 1996). Although temperate forests do not contain the megadiversity of equatorial regions, they are more faunistically complex than might be initially assumed. Thus, simplification and homogenization of forest biota from extensive harvesting are real threats (Siitonen and Martikainen 1994). To humans, losses may include a wide range of values from practical to ethical (Wilson 1986; Bunnell 1991). In response, biologists have begun to describe the range of natural variation within biological systems, with the assumption that this variation can be understood and maintained, even under intensive resource extraction (Kouki 1994; Syrjänen *et al.* 1994).

Recent changes in forest harvesting are characterized by efforts to develop more sustainable use of forests (BC Min. Env./Min. For. 1995). Biological diversity is recognized as a cornerstone in maintaining ecosystem productivity and is valued in its own right. It is thus firmly embedded in current and developing pursuits of sustainable management (Noss and Cooperrider 1994).

"Coarse-filter" approaches to maintaining overall biodiversity are those which seek to maintain pre-harvest levels of biological diversity *via* the maintenance of habitat diversity (BC Min. Env./Min. For. 1995). In forestry, this is pursued at the stand and landscape levels (Coates and Steventon 1995). Various methods of leaving structural retention

within stands during harvesting have been referred to as "Live Tree Retention" (CCEM 1995). These methods, from clearcutting to single tree selection, will contain a range (0-100%) of "old-growth equivalency" (Coates and Steventon 1995). This term is measured in floristic contexts (D. Steventon pers. comm.[1]), and data to examine other taxa are being collected.

Structural retention is thought to provide refuges for organisms during harvesting, sites for colonization-recolonization dynamics as a harvested site regenerates, and foraging and other resources for non-resident organisms like some birds (CCEM 1995). Patch retention, (a.k.a. wildlife tree patches, group retention) is an intermediate form of this concept, cited as having about 25% old-growth equivalency (Coates and Steventon 1995).

Arthropods and especially insects are a dominant contributor to species-level diversity in terrestrial systems (Wilson 1992), but are poorly understood in the context of natural and anthropogenic disturbances (Schowalter 1994, 1995 *a*,*b*). This thesis examines various aspects of ground-dwelling invertebrate communities in temperate coniferous forests, contrasting observed ranges of natural variability with responses to traditional clearcutting and newly created patch retention harvests.

Clearcutting

Clearcutting has been the traditional method of forest harvesting in BC (BC Min. Env./For. 1995). It is efficient in removing large, contiguous tracts of forest in areas of tens to thousands of hectares. This is sometimes termed "even-aged management", as a

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homogenous stand structure is promoted in areas where forests will presumably regenerate. In some forest systems, this type of harvest may be more appropriate than in other systems as it is *relatively* similar to the way in which forest stands are modified by disturbance regimes other than harvesting (BC. Min. Env./ Min. For. 1995). However, the *rate* at which clearcut harvests are proceeding, and the smaller-scale differences between harvests and natural processes gives rise to concern: clearcuts on the order of 40 ha (typical areas in northern BC) are large areas without forest canopy, and thus they lack microclimates associated with contiguous canopy cover. Stand and landscape level patterns from this type of disturbance differ from natural disturbances like wildfire (DeLong and Tanner 1996) and may prohibit essential population processes of forest-dependent organisms. Natural disturbances leave in their wake diverse arrays of habitat attributes, that are absent in clearcut harvesting, especially if practised in a multiple-pass rotation (Coates and Steventon 1995). These elements include coarse-woody debris, standing dead snags, islands of intact forest (Coates and Steventon 1995; Steventon 1994), and burnt substrates with nutrients (Parminter 1983).

Patch Retention

The BC Ministry of Forests has begun to explore alternative harvesting patterns to create and maintain a diversity of stand-level attributes (BC. Min. Env./ Min. For. 1995). When practised over entire landscapes, the additive effects of stand structures are thought to contribute to significantly different large-scale patterns of habitat (Fig. 1) and, presumably to species distributions and associated ecological processes. By landscape, I follow the ideas of three sources. Forman and Godron (1986) offers the following

properties to define the concept of landscape in an ecological sense: "...a distinct, measurable unit defined by its recognizable and spatially repetitive cluster of interacting ecosystems, geomorphology, and disturbance regimes." Landscape ecology should focus on function, structure and change (Forman and Godron 1986).

Hierarchical land classification systems are used widely to prescribe uses for landscapes, based on their ecological qualities. The Biogeoclimatic Ecosystem Classification (BEC), developed for use in British Columbia, is concurrent with these definitions of landscape, in establishing its hierarchical classification of ecosystems based on climate, geomorphology and vegetation (Meidinger and Pojar 1991). My interpretation is that the unit of subzone (see Chapter 2) most closely approximates the sense of landscape from Forman and Godron (1986). "Subzone" refers to a climatically and vegetatively heterogeneous area, constituting variable areas of single to several geological features, such as drainages, mountain ranges, and plateaus (Meidinger and Pojar 1991). A concise working definition for landscape, in the context of conservation

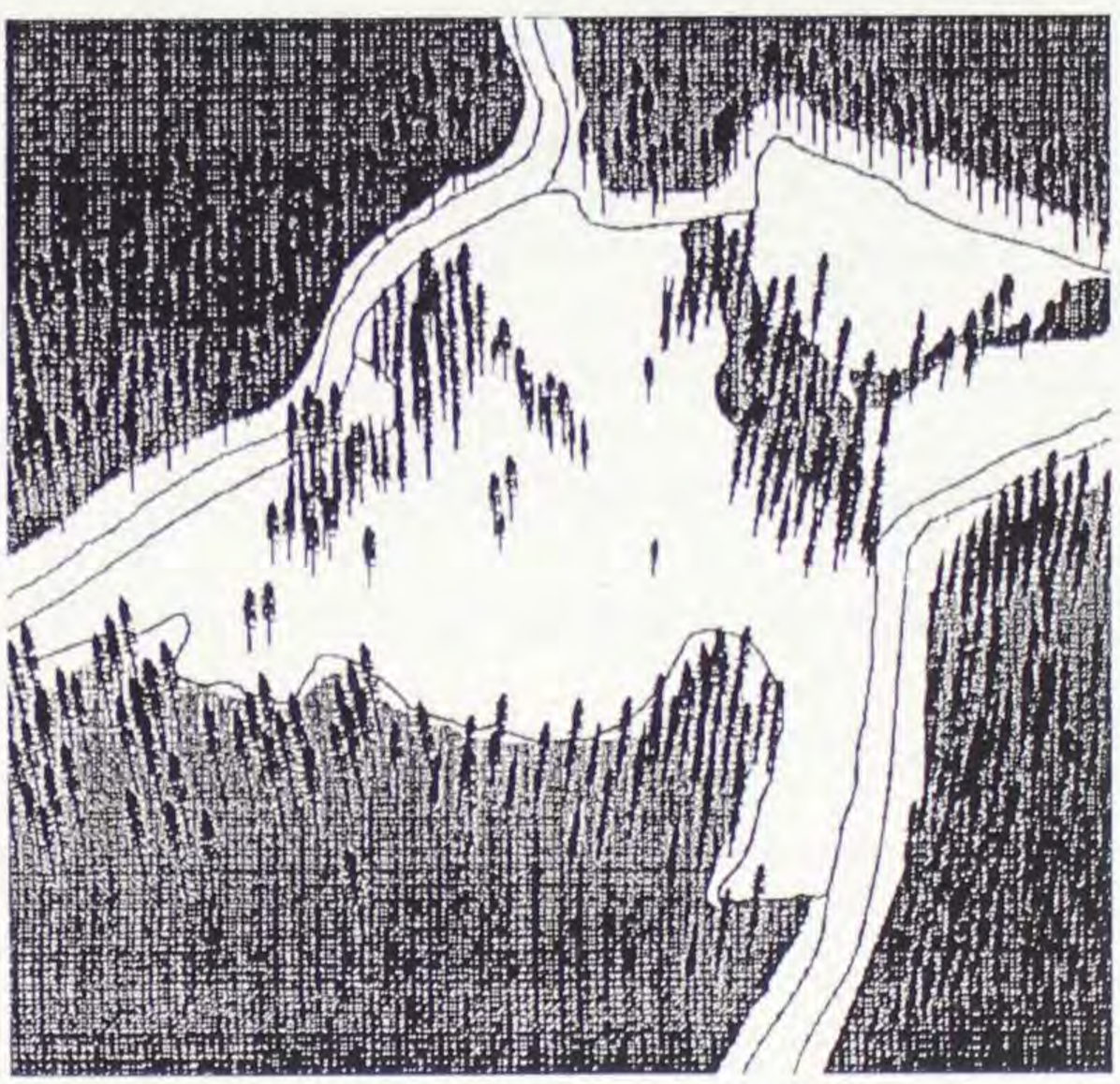

Figure 1. Diagrammatic representation of a patch retention harvest (adapted from Coates and Steventon 1995).

of biological diversity, is given in BC Min. Env./Min. For. (1995): "a watershed or series of similar and interacting watersheds, usually between 10 000 and 100 000 ha in size". Subzone classification using BEC provides a convenient definition of landscape, and an ecological context in which to measure effects at the stand, and smaller levels of scale.

The stand-level disturbances contrasted here are "patch retention" harvesting, and standard clearcut harvesting. The former differs in the retention of small areas of standing timber (0.1-2.0 ha) in amounts comprising 5-20% of a harvest's potential volume (harvests in upper British Columbia are typically in the area of 40-60 ha), (Coates and Steventon 1995). This harvesting regime is initiated in stands where even-aged management is appropriate, and is often referred to as "clearcutting with reserves" (BC Min. Env./For. 1995). Assumedly, this type of disturbance *better* mimics natural disturbance patterns where wildfire has been a prominent stand-initiating agent (Coates and Steventon 1995).

Although much freedom is afforded the harvesting licensee in designing reserves, recommendations are for retention in wetter areas (riparian, wetland and lesser) where diversity and rarity are thought to be highest and where fires might likely have been less intense. Costs of operation are higher with patch retention as increased organization, planning and supervision are required to satisfy design requirements (Hansen *et al.* 1995). Less volume may be available for each harvesting effort (see Coates and Steventon 1995 for a thorough review of theory, policy and practice for this harvesting type).

Patch retention is thought to be able to provide a disturbance regime closer to that found in the absence of forest harvesting. This in turn is assumed to provide large and small-scale habitat that will promote the maintenance and regeneration of pre-harvest biota. These assumptions regarding the effects of patch retention harvesting remain largely untested. Are the costs justified? Will patch retention make a difference to conservation of biological diversity? How should this be measured?

Insects and Ground Beetles

That conservation of habitat diversity is used as an umbrella for biodiversity conservation (BC Min. Env./Min. For. 1995) is strongly a reflection of ignorance regarding many taxa including invertebrates, fungi and microorganisms. Insects, one of several diverse invertebrate groups, have been estimated to number as many as 50,000 species in BC with fewer than half that number described (Cannings 1992). This is compared with 143 species of mammals and about 454 species of bird (BC Min. Env. 1994; Scudder 1996) This estimate espouses ten insect species for every plant species (Cannings 1992). In the Prince Rupert Forest Region, virtually no baseline studies have been performed to assess invertebrates (Radcliffe *et al.* 1994) and there are few documents summarizing distribution of even popular groups, like butterflies, for the Province.

The case for insects and their roles in global biological diversity is even more profound. Insect species comprise over 50% of known organisms (there are about 750,000 described insect species (Wilson 1992) and some estimates are for 80% or higher (Samways 1994). Such estimates do not include microscopic and marine organisms.

However, whatever the species number debate reveals, insects will be present in unidentified millions of species, and be seen to make an appreciable contribution to biotic richness, and diversity.

With basic collections and taxonomic works of insects in their infancies, there is the expected paucity of ecological data for management. This is in marked contrast to the importance of insect taxa, which in terms of species richness and diversity, habitat distribution, and functional roles in ecosystems, is considerable (Samways 1993, 1994).

In the entomological community, the disparity of identifications' expertise is often referred to as "the taxonomic impediment" (Samways 1993); ecologists and others cannot do their work because they simply do not know which organisms they are working with. While there is an increasing need for the foundational sciences of taxonomy, identification and systematics, these disciplines are being phased out of the civil and university systems (Ball and Danks 1993; Scudder 1987). This is a practical and political paradox.

The ground beetles (Coleoptera: Carabidae), is one of the few arthropod groups for which a stable taxonomy has been established, and for which there is a reasonable amount of ecological literature, and quality reference materials to support identifications. This group has been characterized as mainly predatory or oligotrophic with temperate species being primarily surface-dwelling and often nocturnal. These characterizations are based on the conspicuous behaviours of some species, but several detailed investigations point

toward more complex ecologies. For example, *Pterostichus algidus* has been implicated as a pest in consumption of Douglas-fir seeds (Johnson *et al.* 1966), while individuals in the genera *Pterostichus* and *Scaphinotus* have been observed to prey upon animals as large as juvenile salamanders (Ovaska and Smith 1988). Some individuals of *Calosoma* spp. have been observed to frequently climb into forest canopies in search of food (Furniss and Carolin 1977), and investigation of vertical distribution of carabids in a forest floor reveals significant degrees of activity below the litter surface (Loreau 1987).

Approximately 2,200 North American species are known (Borror *et al.* 1989). There are 946 described species in Canada and Alaska with 483 occurring in British Columbia (Bousquet 1991). An excellent taxonomic work exists for the identification of species in Canada and Alaska (Lindroth 1961-1969), including general range descriptions, but only incidental, and often vague habitat descriptions. Overall this group possesses a relatively rich status in the literature, lending it very well to study. For temperate forestry issues, it has several other desirable qualities:

- Being active in the litter layer of temperate regions, carabids are easily trapped.
- Impacts of forest harvesting are not implicit as some potential habitat characteristics will remain intact with canopy removal.
- Ground beetles are abundant and diverse in most ecological systems and therefore serve as an appropriate group for which to make inter-regional comparisons.

- Foremost, ground beetles are an invertebrate, ecological, and taxonomic entity and may be used for contrast with the much larger body of knowledge established for the relatively few species of higher animals, and plants in the province.

In evidence of the quality of these criteria is a considerable body of work focused on the ecology of this group in forested and agricultural habitats. Many recent conservation works have focused on forest litter-dwelling fauna (Craig 1995; Halme and Niemelä 1993; Lenski 1982; McIver *et al.* 1990; Niemelä and Spence 1994; Niemelä *et al.* 1996, 1993, 1992; Pajunen *et al.* 1995; Punttila *et al.* 1994; Spence *et al.* 1996; Sustek 1981; Walsh *et al.* 1993), apparently for the reasons outlined above. Groups like Carabidae, Araneae, and Staphylinidae (occasionally the Formicidae) receive attention because they are convenient to capture. How well they can be used to answer ecological and conservation questions, as compared to other invertebrate groups is an issue unexplored. Concurrent ease of sampling for these groups belies their mutual habits: many species are mobile predators in the litter layer and at the litter surface (hence a high frequency of encounter with traps in that stratum). For Carabidae, specificity toward singular habitats is questionable, and thus the precision of measurement they are able to provide about effects upon the rest of invertebrate faunas that are more specialized, is also dubious. How will land use decisions, which conserve the diversity of generalist arthropod species, affect other ecological groups? This issue is deserving of exploration and research, but trapping methods and taxonomic keys to proceed in this direction do not exist. I will use results from this study to further demonstrate need in this regard. Nonetheless, the

established literature for the pitfall fauna provides a strong basis to refine understanding of relationships between land use and some specific invertebrate groups.

Objectives

This study examines the distribution and composition of ground beetle assemblages in two forest harvesting types: traditional clearcut harvests and patch retention harvests. The broad objectives are:

- To develop a trap design/collection fluid combination for efficient monitoring in large-scale efforts.
- To understand stand-level habitat disturbance in terms of effects on carabid beetles and provide a comparison of distributions through patch retention and clearcut harvests.
- To provide further baseline knowledge about distribution of this group in north central British Columbia.

The following work is divided into three chapters, the first two addressing accessory issues needed to support the methods used to address effects of harvesting treatment in Chapter 3:

- A comparison of trapping efficiency between a modified trap design used here and standard pitfall trap design, and between ethylene glycol and brine as preservative media.

- An examination of the degree to which ground beetle assemblages are predicted by the occurrence of "small scale" habitat classifications. This will establish the natural range of variability for this group in the chosen forest type, before proceeding to an examination of harvesting effects in Chapter 3.

Bibliography

Ball, G. E., and H. V. Danks. 1993. Systematics and Entomology: Introduction. pp. 3-10 *in*: Ball, G. E., and H. V. Danks, eds. *Systematics and Entomology: Diversity, Distribution, Adaptation, and Application.* Memoirs of the Entomological Society of Canada, No. 165.

BC Min. Env. 1994. *British Columbia Terrestrial and Freshwater Invertebrates: Inventory Priorities for and Status of Rare and Endangered Species.* BC Min. Env.- Wildlife Branch, Victoria, BC.

BC Min. Env./Min. For. 1995. *Biodiverstiy Guidebook.* Forest Practices Code Guidebooks. Province of BC, Victoria, BC.

Borror, D. J., C. A. Triplehorn, and N. F. Johnson. 1989. *An Introduction to the Study of Insects*. 6th ed. Toronto: Saunders College Publishing.

Bousquet, Y. 1991. *Checklist of Beetles of Canada and Alaska*. Ottawa. Ont.: Agriculture Canada, Publication 1861/E.

Bunnell, F. L. 1991. Biodiversity: what, where, why, and how. pp. 29-45 *in*: *Proceedings, Wildlife Forestry Symposium.* Victoria, BC, For. Can. / BC Min. For.

Cannings, S. 1992. Arthropods - where diversity is really at. pp. 43-48 *in*: Ramsey, L. R., ed. *Methodology for Monitoring Wildlife Diversity in BC Forests.* BC Environment, Wildlife Branch, Victoria BC.

CCEM (Cascade Center for Ecosystem Management). 1995. *Residual Trees as Biological Legacies.* Communique 2. CCEM, Corvallis, OR.

Coates, D. K., and D. J. Steventon. 1995. Patch retention harvesting as a technique for maintaining stand level biodiversity in forests of north central British Columbia. pp. 102-6 *in*: Bamsey, C. R., ed. *Innovative Silvicultural Systems in Boreal Forests.* Conference Proceedings, October 2-8, 1994, Edmonton, AB. Clear Lake Ltd., Edmonton, AB.

Craig, K. G. 1995. Variation in Carabid Community Structure Associated with Coastal Douglas-fir Forest Successional Stages. M.Sc. Thesis, University of British Columbia, Dept. Zool. Vancouver, British Columbia.

Delong, S. C., and D. Tanner. 1996. Managing the pattern of forest harvest: lessons from wildfire. *Biodiversity & Conserv.* 5: 1191-205.

Forman, R. T. T., and M. Godron. 1986. *Landscape ecology*. USA: John Wiley & Sons, Inc.

Furniss, R. L., and V. M. Carolin. 1977. *Western Forest Insects*. Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture: Miscellaneous Publication No. 1339.

Halme, E., and J. Niemelä. 1993. Carabid beetles in fragments of coniferous forest. *Ann. Zool. Fenn.* 30: 17-30.

Hansen, A. J., S. L. Garman, J. F. Weigand, D. L. Urban, W. C. McComb, and M. G. Raphael. 1995. Alternative silvicultural regimes in the Pacific Northwest: simulation of ecological and economic effects. *Ecol. Appl.* 5: 535-54.

Johnson, N. E., W. H. Lawrence, and I. D. Ellis. 1966. Seasonal occurence of ground beetles (Coleoptera: Carabidae) in three habitats in southwestern Washington. *Ann. Ent. Soc. Am.* 59 (6): 1055-59.

Kouki, J. 1994. Biodiversity in the Fennoscandian boreal forests: natural variation and its management. *Ann. Zool. Fenn.* 31 (1): 1-217.

Lenski, R. E. 1982. The impact of forest cutting on the diversity of ground beetles (Coleoptera: Carabidae) in southern Appalachians. *Ecol. Ent.* 7: 385-90.

Lindroth, Carl. H. 1961-1969. *The Ground-Beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska*. (Suppl.) 20 (1961), 24 (1963), 29 (1966), 33 (1968), 34 (1969), & 35 (1969). Lund University, Sweden: Opuscula Entomologica.

Loreau, M. 1987. Vertical distribution of activity of carabid beetles in a beech forest floor. *Pedobiologia* 30: 173-78.

McIver, J. D., A. R. Moldenke, and G. L. Parsons. 1990. Litter spiders as bio-indicators of recovery after clearcutting in a western coniferous forest. *Northwest Environ. J.* 6 (2): 410-412.

Meidinger, D., and J. Pojar. 1991. *Ecosystems of British Columbia*. Special Report Series Number 6. BC Ministry of Forests, Victoria, BC.

Niemelä, J. K., and J. R. Spence. 1994. Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. *Ecography* 17: 166-75.

Niemelä, J., Y. Haila, and P. Puntilla. 1996. The importance of small-scale heterogeneity in boreal forests: variation in forest-floor invertebrates across the succession gradient. *Ecography* 19: 352-68.

Niemelä, J., D. Langor, and J. R. Spence. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in Western Canada. *Conserv. Biol.* 7 (3): 551-61.

Niemelä, J., J. R. Spence, and D. H. Spence. 1992. Habitat associations and seasonal activity of ground-beetles (Coleoptera, Carabidae) in central Alberta. *Can. Ent.* 124: 521-40.

Noss, R. F., and A. Y. Cooperrider. 1994. *Saving Nature's Legacy - Protecting and Restoring Biodiversity*. Washington DC, USA: Island Press.

Okland, B. 1995. Diversity patterns of two insect groups within spruce forests of southern Norway. Agricultural University of Norway. Inst. for biologi og naturforvaltning norges landbrukshogskole Postboks 5014, N-1432 Ås Norsk institutt for skogforskning Hogskolevn.

Ovaska, K., and M. A. Smith. 1988. Predatory behavior of two species of ground beetles (Coleoptera: Carabidae) towards juvenile salamanders (*Plethodon vehiculum*). *Can. J. Zool.* 66: 599-604.

Pajunen, T., Y. Haila, E. Halme, J. Niemelä, and P. Punttila. 1995. Ground-dwelling spiders (Arachnida, Araneae) in fragmented old forests and surrounding managed forests in southern Finland. *Ecography* 18: 62-72.

Parminter, J. 1983. Fire history and fire ecology in the Prince Rupert Forest Region. pp. 1-36 *in*: Trowbridge, R. L., and A. Macadam., eds. *Prescribed fire: forest soil symposium.* BC Ministry of Forests, Land Management Rep. 16, Victoria, BC.

Punttila, P., Y. Haila, J. Niemelä, and T. Pajunen. 1994. Ant communities in fragments of old growth taiga and managed surroundings. *Ann. Zool. Fenn.* 31 (1): 131-44.

Radcliffe, G., B. Bancroft, G. Porter, and C. Cadrin. 1994. *Biodiversity of the Prince Rupert Forest Region.* Land Management Report. BC Ministry of Forests, Victoria, BC.

Samways, M. J. 1994. *Insect Conservation Biology*. London UK: Chapman & Hall.

Samways, M. J. 1993. Insects in biodiversity conservation: some perspectives and directives. *Biodiversity & Conserv.* 2: 258-82.

Schowalter, T. D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. *For. Ecol. & Mgt.* 78: 115-25.

Schowalter, T. D. 1995. Canopy invertebrate community response to disturbance and consequences of herbivory in temperate and tropical forests. *Selbyana* 16 (1): 41-48.

Schowalter, T. D. 1994. Invertebrate community structure and herbivory in a tropical rain forest canopy in Puerto Rico following hurricane Hugo. *Biotropica* 26 (3): 312-19.

Scudder, G. G. E. 1987. The next 25 years: invertebrate systematics. *Can. J. Zool.* 65: 786-93.

Scudder, G. G. E. 1996. *Terrestrial and Freshwater Invertebrates of British Columbia: Priorities for Inventory and Descriptive Research.* Working Paper 09/1996. Province of British Columbia, Ministry of Forests Research Program, Victoria, B.C. Canada.

Siitonen, J., and P. Martikainen. 1994. Occurence of rare and threatened insects living on decaying *Populus tremula*: A comparison between Finnish and Russian karelia. *Scand. J. For. Res.* 9: 185-91.

Spence, J. R., D. W. Langor, J. K. Niemelä, H. A. Càrcamo, and C. R. Currie. 1996. Northern forestry and carabids: the case for concern about old-growth species. *Ann. Zool. Fenn.* 33: 173-84.

Steventon, J. D. 1994. *Biodiversity and forest management in the Prince Rupert Forest Region: A discussion paper.* BC Min. For. Land Man. Rep. #82. Victoria, BC.

Sustek, Z. 1981. Influence of clear cutting on ground beetles (Coleoptera, Carabidae) in a pine forest. *Communicationes Instituti Forestalis* 12: 243-54.

Sutton, S. L., T. C. Whitmore, and A. C. Chadwick. 1983. *Tropical Rain Forest: Ecology and Management.* Oxford: Blackwell Scientific Publishing.

Syrjänen, K., R. Kalliola, A. Puolasmaa, and J. Mattsson. 1994. Landscape structure and forest dynamics in subcontinental Russian European taiga. *Ann. Zool. Fenn.* 31 (1): 19-34.

Walsh, P. J., K. R. Day, S. R. Leather, and A. Smith. 1993. The influence of soil type and pine species on the carabid community of a plantation forest with a history of pine beauty moth infestation. *Forestry* 66 (2): 135-45.

Wilson, E. O., ed. 1986. *Biodiversity*. Boston: Harvard University Press.

Wilson, E. O. 1992. *The Diversity of Life*. Cambridge, MA: Belknap Press.

Winchester, N. N., and R. A. Ring. 1996. Centinelan extinctions: extirpation of northern temperate old-growth rainforest arthropod communities. *Selbyana* 17 (1): 50-57.

Chapter 1. Experimental Comparison of Trap Design and Collection Media in Pitfall Trapping.

Abstract

A modified pitfall trap design with an integrated lid is proposed for use in large-scale invertebrate trapping regimes, and tested against a standard, open-topped design for efficiency of trapping Carabidae. Its design benefits include ease of use and restriction of rainwater, small vertebrate tampering, and consumption of contents by large vertebrates. Catches of only two of seven common carabid species were significantly affected by trap design: *Calathus advena* Lec. occurred more frequently (mean=7.15 vs. 2.10) in a standard, open-topped trap design and *Elaphrus americanus* Dej. was captured more frequently by the modified design (mean=1.45 vs. 0.76). Cluster analysis, based on Bray-Curtis index of percent similarity, differentiated between assemblages caught in trap designs but did not differentiate between collecting media. For small vertebrate animals (amphibians), occurrences were almost entirely restricted to standard, open-topped traps (12 vs. 1). Dilution of collection media *via* rainwater was reduced in the modified trap design. Ethylene glycol and brine were compared with respect to trapping efficiency of Carabidae. No differences in carabid beetle catch were observed. Specimen condition however, was markedly improved with the use of ethylene glycol, particularly where solution dilution from rainwater occurred. Use of the antifreeze solution was not associated with rates of vertebrate disturbances to traps. Based on the results, the use of the modified design, in conjunction with glycol-based preservatives, is recommended for large-scale, ecologically-oriented trapping.

Introduction

Due to their simplicity and low cost, pitfall traps have become the sampling method of choice for investigators interested in terrestrial arthropods. The original design is an open-topped cylinder buried with the top flush to the ground (Barber 1931; Hertz 1927). Round containers of this nature are extremely convenient, and according to Spence and Niemelä (1994) are generally more efficient than ramp or gutter traps (rectangular in shape). Variations in basic design include size (perimeter) and shape (Adis 1979; Luff 1975; Morrill *et al.* 1990; Spence and Niemelä 1994), construction material (Luff 1975) as well as the addition of covers (Fichter 1941; Craig 1995; Spence and Niemelä 1994), guides and barriers (Craig 1995; Holopainen and Varis 1986; Morrill *et al.* 1990; Southwood 1978), removable inner cups (Spence and Niemelä 1994) and mesh screens (Morrill *et al.* 1990; Niemelä *et al.* 1992; van den Berghe 1992).

Trap design, among other factors, is known to interact uniquely with a given species, but in general the resulting catch is a linear (but undetermined) function of actual animal density (Baars 1979). Adis (1979) stresses the need for a standardization of trap design to enable the synthesis of data between studies, even to the extreme of developing a design and testing centre. While this notion has some appeal, I believe that designs will continue to be determined at least in part by the specific needs/limitations of a particular investigation.

One objective for this study was to provide a tool for monitoring ground arthropods that is as easy as possible to install and maintain. Operational trapping at large spatial scales would require that traps: 1) are lightweight, 2) are stackable, 3) minimize vertebrate entrances and tampering, and 4) minimize effects of weather on samples (rainfall accumulation or desiccation from heat). A convenient but unorthodox trap design with integrated lid and circular entrances in the container side-wall is introduced here.

Preservatives are often used in pitfall traps to minimize the problem of specimen decay and predation, as well as to increase trapping efficiency by reducing frequency of escapes. Alcohol (Luff 1968; Southwood 1978), formalin (Holopainen and Varis 1986; Luff 1968; Petruska 1969), phenyl mercuric acetate (Macfayden 1963, referenced in Luff 1968), and ethylene glycol (Holopainen 1992; van den Berghe 1992) are frequently used. Depending on the objectives of a particular study, an investigator may wish a preservative to have varying degrees of the following qualities: 1) render clean, high quality specimens; 2) remain non-volatile; 3) remain effective when diluted by rainwater or concentrated by evaporation; 4) be cheap; 5) accessible; 6) non-toxic; 7) unattractive to vertebrates; and 8) neutral with regard to attracting invertebrates. Only number 8 has received attention in the literature (Greenslade and Greenslade 1971; Holopainen 1990, 1992; Holopainen and Varis 1986; Luff 1968; Waage 1985) because possible trapping biases from the use of preservatives has been a priority issue for users of pitfall method.

For the the larger work of this study (Chapter 3) I used concentrated brine (as recommended by van den Berghe 1992), as a preservative in pitfall traps for the first of

two years of sampling, but found it to have several disagreeable qualities. Brine is inexpensive and easily available, but with extended trapping intervals of three weeks or more it was unsatisfactory as a preservative. In 1996, ethylene glycol was substituted for brine. Ethylene glycol is relatively cheap and available commonly as automobile antifreeze. It is relatively non-volatile and will continue to retard decomposition, even when strongly diluted with water (J. Spence[1], pers. comm.). However, it is quite toxic to domestic vertebrates and humans (Hall 1991), and has been implicated as an attractant to vertebrates (Marshall and Doty 1990) and invertebrates (Holopainen 1992).

Because of the unorthodox pitfall trap design, and the change in trapping fluid from year to year, a trial was conducted to examine possible effects of design and collection fluid on carabid catches. I wished to test the broad hypothesis that there is no statistically significant difference in carabid species' abundance, or assemblage patterns, that can be ascribed to either trap design or collection fluid. As well, I wished to investigate the occurrence of gastropods and vertebrates among treatments. Both of these groups are undesirable (gastropods because they expel a thick mucous into samples, making the collection, sorting and cleaning of specimens difficult, and both of these groups because they can advance sample deterioration and alter trap catches (van den Berghe 1992)). From a conservation perspective, the reduction of vertebrate mortality in traps is desirable.

Lastly, I comment on operational issues associated with this particular trap/fluid combination. Although no disturbances associated with large vertebrates occurred in this

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comparative study, they have been common in my wider work (see Chapter 3). Disturbed traps were variously lifted out of the ground, turned upside down, chewed, demolished and occasionally missing from a site altogether. The switch of preservatives between seasons gave rise to concern that disturbances would increase, associated with attractive qualities of ethylene glycol to vertebrate animals. I used these data to evaluate trap disturbances from large vertebrates as influenced by collection fluid.

Aspects of the Nordlander (1987) design as well as the preservative advantage of ethylene glycol are discussed in the context of fluid evaporation and dilution *via* rainwater.

Methods and Materials

Trap design and placement.

Nordlander (1987) used a modified design, which is easy to install and maintain, for monitoring a forest pest insect. This design catches Carabidae of all sizes (S. Lindgren[2], pers. comm.), is convenient and inexpensive, and provides many advantages over others commonly used. I chose this design for the work produced throughout this study. This modified design was compared with a conventional pitfall trap (Fig. 2).

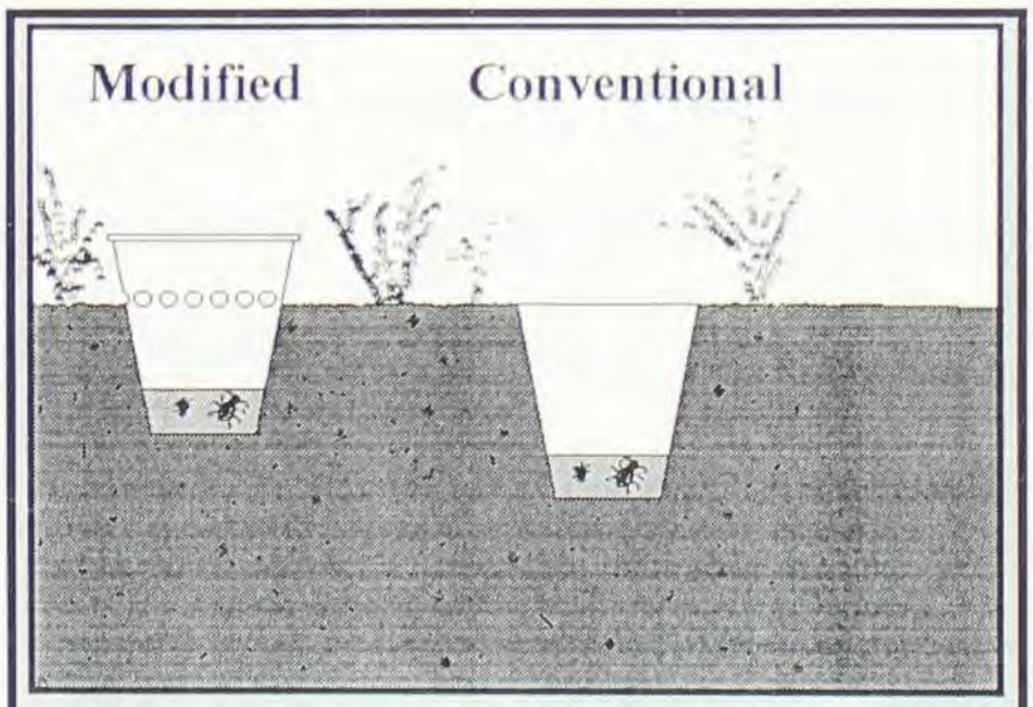

Figure 2. Modified pitfall trap design used in study near Smithers, BC and conventional design commonly used elsewhere.

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One-litre, white high-density polyethylene containers with lids (Genpac™, Toronto-Cookshire, Ontario, Canada), were used in trap construction. Traps were slightly conical (allowing stacking) and had the following dimensions: top/bottom diameters of 11.5/ 9 cm, respectively; height of 12 cm.

Containers were modified by drilling fifteen holes of 1.3 cm diameter around the container circumference, 2 cm below the upper rim, using a standard drill press and high-quality wood bit. Plastic cup inserts, constructed from severed bottoms of trap containers, were placed in the bottom of each trap before adding fluid. This inner cup was 5 cm in height and removable, allowing the main trap body and surrounding habitat to remain undisturbed when emptying traps (Spence and Niemelä 1994). Active trap circumferences (potential area where specimens could enter traps) for the Nordlander vs. the standard trap design, were 15.0 and 36.1 cm, respectively (ratio of 1.0: 2.4).

Experimental design and implementation.

Traps were inserted into the ground with a soil auger of a diameter slightly smaller than the widest diameter of the trap. Insertions were made with a twisting motion, pushing away the surrounding soil, and providing a snug fit between ground and trap. When modified traps were placed, lids were left on containers, which were buried with holes nearly flush to the ground and about 3 mm of hole extending beneath the surface. Conventional traps were placed likewise but without a lid and inserted until the rim of the container was flush to the ground surface. Collection fluids were ethylene glycol (Prestone™ automobile antifreeze) or water, super-saturated with rock salt. Saturation

was obtained by adding salt to water while stirring in a 20 litre container, at ambient air temperature (about 20°C). A few drops of dish detergent (unscented, aqua-coloured generic brand purchased from Canada Safeway™, Smithers, BC) were added to the latter. This is thought to reduce escape rates from water-based collecting media by reducing surface tension of the collection media (Basedow 1976). Approximately 200 ml of fluid preservative was added to the inner cup of each trap.

The experimental site was in a clearcut/broadcast-burned area in a valley bottom near Smithers, BC, and proximal to harvested areas surveyed in my wider work. A clearcut site was deemed most accessible, and from 1995 experience, would produce abundant and diverse carabid captures to address the experimental hypotheses. To mitigate potential microsite influences, the area was chosen because it possessed a homogeneous habitat structure of grasses, shrubs and burnt wood (qualitative assessment).

Forty traps were arranged in a completely randomized design. Blocking was not used because it reduces the power of analysis, and no environmental features could be distinctly identified with which to block. Each treatment, conventional (Barber 1931) and modified (Nordlander 1987) trap design, had two levels, corresponding to collection fluids. Traps were operated from 24 July to 11 September 1996, with collections at two-week intervals. Latex laboratory gloves were used for all phases of collections, to avoid contact of skin with ethylene glycol. If fluids were diluted or contaminated at a collection interval, they were replaced. Catches were strained through two layers of 10 x 10 cm cotton gauze and labelled with a piece of water-proof paper, placed in with trapped

contents. The corners of the gauze were drawn up to make a small pouch and tied with a small piece of wire, or "twist tie". Samples were removed to the laboratory for sorting, species determinations, and enumeration.

Samples were washed gently using dish detergent and warm water and then rinsed.

Carabid beetles, gastropods and vertebrates captured in each trap were tallied.

Analysis.

To test for trap design and fluid effects on a species-by-species basis, most data were subjected to a two-factor ANOVA (Systat™ 1997). Data were log transformed to meet the normality and variance-homoscedasticity assumptions of this procedure (Zar 1984). In cases where transformed data did not meet parametric ANOVA assumptions, single-factor Kruskal-Wallis non-parametric ANOVA tests were used (Zar 1984), accompanied by single-factor parametric ANOVA for the accompanying factor (trap design or fluid type), which did meet parametric assumptions. Calculation of the Bray-Curtis index of percentage similarity (Bray and Curtis 1957) was made for total catches of each treatment combination and subjected to average-linkage cluster analysis (Pielou 1984). This index is a simple measure of similarity based on species-abundance values from two comparable assemblages. The index, C_N, is calculated as follows:

$$C_N = \frac{2\,jN}{(aN + bN)}$$

Where jN is is the sum total of individuals common to both samples a and b. The quantities aN and bN represent the sum of all species collected for those samples,

respectively. A second analysis was made, with the removal of two species that had shown significant ANOVA differences between trap designs. This allowed for an examination of the degree of influence these species were exerting on the dendrogram structure.

To test for effects of fluid on trap disturbances by large vertebrates, data from trapping described in Chapter 3 were analyzed with a G-test, performed by hand (Zar 1984).

Results

Observations of preservative performance.

Most Coleoptera were well preserved in brine, with the exception of Staphylinidae, which were often dissociated. Other taxa, such as Araneae, fared even less well. Salt deposits were frequent on some specimens. Large numbers of Gastropoda were captured, and I suspected these to have been attracted by the brine. Slugs evidently expelled large amounts of mucous, contaminating trap catches. [In addition, previous experience showed that brine corroded metal equipment (vehicle bed, fire-extinguishing tanks used to dispense collection fluids, *etc.*).] Brine needed replacing every two weeks, and thus limited the interval period for collections. Alternatively, antifreeze preserved all types of invertebrates very well. Previous trapping experience has shown that ethylene glycol can be used for collection periods of 4 weeks and more in the environment in which the study was performed (see Chapter 3).

Carabid catches.

Thirteen species of Carabidae were caught, and seven of these were abundant enough for analysis by ANOVA (Table 1). Of the total catch, 89.5% was composed of five common species. At the α=0.05 level of significance, only two species, *Calathus advena* Lec., and *Elaphrus americanus* Dej. showed a significant response to trap design ($p<0.001$; $p=0.042$, Table 1), with higher and lower average catches in the Barber (1931) design, respectively. Catches of *Trechus chalybeus* Dej. had a p-value of 0.059 (Table 1), with a higher average catch for the Nordlander (1987) design. No species were significantly affected by trap fluid. Overall carabid catch (all species' catches pooled) was unaffected by treatment.

Cluster analysis (based on all thirteen species) differentiates between trap design first and shows assemblage patterns consistently different from one another (Fig. 3), with an average Bray-Curtis percent similarity of 37.8% between all samples. All splits in the dendrogram occurred within eight percentage points, indicating that trap design influenced catches only slightly more than fluid type.

Gastropod and vertebrate catches.

Gastropods were more than twice as numerous as Carabidae and did not respond significantly to either treatment (Table 1). Qualitatively, neither my field assistant nor I could distinguish between the unacceptably large amounts of mucous expelled into either liquid.

Table 1. Mean ± SE catch of commonly occurring taxa in experiment examining effects of pitfall trap design and preservative fluid (n=20 for all treatment categories; 40 observations total).

Taxon	Total Catch (all traps)	Mean (# individuals/trap, all collection dates pooled) ± SE				ANOVA probability		
		Trap Type		Fluid Type		Trap Effect	Fluid Effect	Trap*Fluid Interaction
		Standard	Modified	Brine	Ethylene Glycol			
Pterostichus riparius Dej.	219	5.45 ± 1.33	5.50 ± 1.15	5.10 ± 1.36	5.80 ± 1.12	0.866	0.426	0.685
Calathus advena Lec.	185	7.15 ± 1.45	2.10 ± 0.40	4.65 ± 1.25	4.60 ± 1.16	**0.001**	0.446	0.213
Scaphinotus marginatus Fisch.	112	2.80 ± 0.93	2.80 ± 0.54	2.25 ± 0.34	3.35 ± 1.01	1.000	0.680**	NA
Trechus chalybeus Dej.	93	1.70 ± 0.47	2.95 ± 0.55	2.35 ± 0.50	2.30 ± 0.55	0.059	0.761	0.230
Pterostichus adstrictus Esch.	91	2.20 ± 0.92	2.35 ± 0.45	1.70 ± 0.41	2.85 ± 0.92	0.353	0.214	0.724
Elaphrus americanus Dej.	37	0.40 ± 0.311	1.45 ± 0.76	0.60 ± 0.47	0.50 ± 0.24	**0.042****	0.289	NA
Agonum metallescens Lec.	16	0.40 ± 0.134	0.40 ± 0.134	0.30 ± 0.13	0.50 ± 0.14	1.00	0.257	0.812
Carabidae	812	22.15 ± 3.33	18.45 ± 1.91	18.45 ± 2.11	22.15 ± 3.21	0.526	0.484	0.781
Gastropoda	1855	50.25 ± 9.08	42.50 ± 5.89	51.15 ± 8.64	46.20 ± 6.46	0.896	0.478	0.889

** Indicates that analysis was performed with non-parametric Kruskal-Wallis ANOVA

Large-vertebrate disturbances from other trapping regimes.

A ratio of numbers of disturbed traps to total trap days, taken from my wider work (see Chapter 3), was used to compare disturbance frequency between years (and hence between brine and ethylene glycol as collection fluids). In 1996, the ratio was 40: 34, 209; or 0.001: 1. In 1995, 16: 13, 186; or 0.001: 1. A G-statistic (Zar 1984) testing independence of trap year (fluid type) and disturbance ratios was calculated, yielding $p>0.999$. Fluid type was found to have no effect upon disturbance frequency.

Fourteen individuals of three species of Amphibia were captured in traps including the following: 9 *Bufo boreus*, 2 *Rana* spp., and 3 *Ambystoma macrodactylum*. With the exception of one small *B. boreus*, all of these occurred in conventional, open-topped traps.

Rainfall accumulation.

Two weeks seemed an optimal collection interval for open-topped traps as they had accumulated rainwater, sometimes to the brim but never overflowing. The Nordlander (1987) design accumulated comparatively little water. If traps were not placed in depressions, collection interval length would be limited only by preservative qualities of the collection fluid.

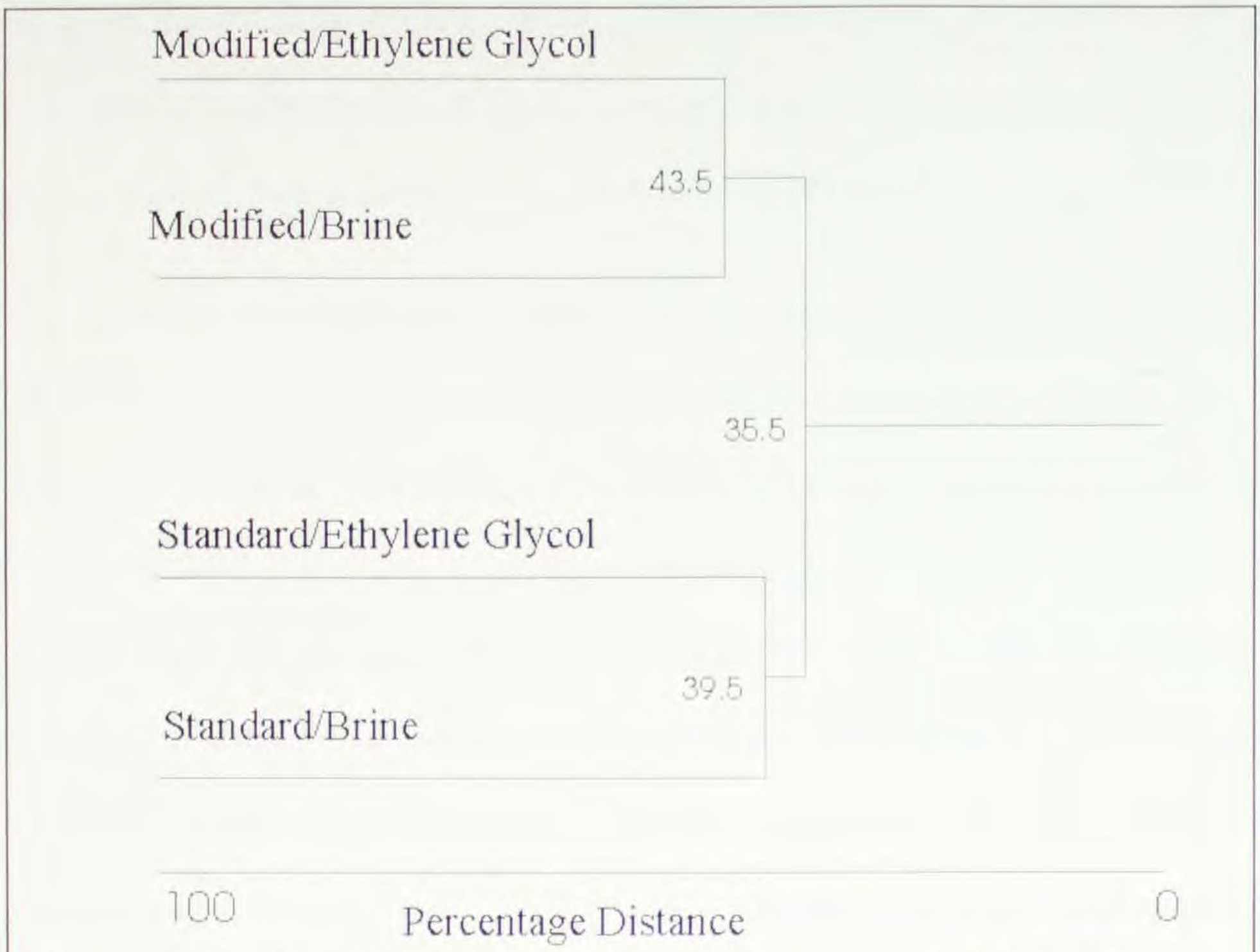

Figure 3. Cluster diagram based on pitfall comparisons with Bray-Curtis index of percentage similarity. Clusters are labeled according to Trap/Fluid combinations constituting treatments. "Standard" and "Modified" refer to Barber (1931) and Nordlander (1987) designs, respectively.

Discussion

Trap design.

The meager responses of carabids to treatment types were unexpected, based on previously reported results. The null hypothesis of no effect for trap design is rejected only for two species, the results of which are contrary. Cluster analysis did however strongly differentiate assemblages caught among treatment types. All treatment combinations were only about 40% similar. In addition, *T. chalybeus* catches approached significance in favour of the Nordlander (1987) trap design. This species was much less

numerous than *C. advena*, and it is possible that the null hypothesis would have been rejected for *T. chalybeus* as well, given increased replication or an extended trapping period. Still, the effects of trap design seem to be variable and species-specific.

An explanation for the differential catches of *C. advena* is not straightforward. Thiele (1977) has implicated tarsal structure as a sexually dimorphic factor responsible for differential sex catches of Carabidae. Males, which sometimes have a more developed serration, are thought to escape from traps more readily than females. Spence and Niemelä (1994) attribute the differential occurrence of *C. ingratus* Dej. in ramp traps to be a function of denticulate tarsal claws in *Calathus* Bonelli. Within this context, the Nordlander (1987) design may be less efficient in two manners. First, it has sharp, rough-cut edges that may be easy to cling to, allowing beetles to avoid initial capture into the trap. In most cases however, beetles would only contact the ground surface before falling into the trap, because the actual surface of the container at each hole is buried slightly below ground level. For imperilled beetles, the ground surface at the entrance of each hole could be a more convenient attachment than plastic surfaces. Second, the placement of the Nordlander traps is shallower in the ground, reducing the distance between fluid surface and trap perimeter found in the standard design (meaning a reduced scaling distance for animals climbing the trap wall). The use of a collecting preservative, however, should reduce this effect, as beetles would be unlikely to scale the surface when wet, or subdued with preservative.

The perimeter effect might also be observed as a species-specific phenomenon. This may be the case with *C. advena*, indicating some trait (e.g. fast versus slow rates of travel,

agility, or quality of vision or smell) predisposing certain populations to capture with the Barber (1931) design.

The Barber (1931) design is often supplemented by the addition of covers to exclude rain (Bostanian *et al.* 1983; Craig 1995; Holopainen 1990, 1992; Honek 1988; Kharboutli and Mack 1991; Mitchell 1963; Petruska 1969; Spence and Niemelä 1994; Southwood 1978; van den Berghe 1992). This is accomplished in the Nordlander (1987) design by the addition of a pre-formed plastic lid, designed specifically for the trap container. Both lid modification types would be conspicuous and perhaps alarming to some species when approaching traps. And indeed, Spence and Niemelä (1994) have demonstrated a reduced capture rate for carabid beetles with the addition of trap covers to pitfall traps, although this effect was variable among habitat types and analysis methods.

The genus *Elaphrus* Fabricius has 14 species in North America, all of which are heliophilous, hygrophilous, and dextrous hunters with well-developed eyesight (Lindroth 1961). Higher catches for *E. americanus* in the Nordlander (1987) design may follow an explanation contrary to that provided above for the effects of trap roofs. The improved eyesight in this group might allow the detection and avoidance of a large, open space like that provided with a Barber (1931) design. Alternatively, the type of entrance provided by the Nordlander (1987) design (a small, cavernous hole) could be deemed an attractive physical feature, worth exploration in foraging, denning, oviposition, *etc*.

Unease with design may arise if one suspected assemblages to be severely biased or species to be absent from catches, especially if a more effective method were easily

available. Data presented here oppose such suspicions and support the use of convenient design against needs for design standardization. This is especially true considering that even with trap standardization, interstudy comparisons would be confounded by differing study objectives and sampling regimes (i.e. trap numbers and configurations).

Spence and Niemelä (1994) have shown that between-design catch comparisons can vary among habitat types. They found that a meadow environment, when compared with several forested habitats, yielded fewer statistical differences between very different kinds of traps (ramp, gutter and round designs). The clearcut sampled here may be considered similar to a meadow (no tree cover, substantial herbaceous ground cover). Thus, the conclusions from my data should be applied to forested habitats with caution, *i.e.*, differences could be somewhat more pronounced. Spence and Niemelä (1994) still indicate at least three species, as well as the total carabid catch, as significantly responsive to different trap types in meadow habitat, lending support to this environment as giving representative data in systematic trap-type comparisons. A large proportion of the trapping in the main study occurred in clearcuts and in forested plots with similar proportions of shrub and herb layer coverage. For Carabidae, the Nordlander (1987) design appears as efficient as open-topped round traps, and in terms of assemblage data, does not have any predictable effect.

Collection fluid.

Holopainen (1990, 1992) demonstrated that ethylene glycol, when compared to water with soap and small quantities of salt, can influence pitfall trap catches for several

arthropod groups, especially carabid beetles. These differences included overall carabid catches, abundance of particular species, and sex ratios within species. The author presents data from two trapping seasons (Holopainen 1992) and showed five carabid species' abundance to be higher when trapped with ethylene glycol as compared to water. Those results, however, were inconsistent from year to year since only a single species demonstrated this effect in both sampling seasons. Adis and Kramer (1975), proposed that catch increases due to formaldehyde preservative could be due to chemical similarity with naturally-occurring compounds, detected by carabids. This seems a plausible explanation for these types of effects, as semiochemical perception is known to be important in the ecology of many insect species.

Holopainen (1992) concluded that ethylene glycol-based catches are more efficient and therefore not comparable with those of water, and he found incidental support in other studies for this conclusion (Helenius 1990; Niemelä *et al.* 1987). I am unable to corroborate these findings at the α=0.05 significance level, and draw attention to logistical differences between our studies. 1. I used saturated brine as a water treatment, which could act as a repellent. Holopainen (1990, 1992) used only a 1% NaCl solution to retard bacterial growth. 2. I used undiluted antifreeze (which is almost pure ethylene glycol) and other studies have used a 50:50 mixture with water, which could be a more attractive concentration for carabids. However, in many instances, my traps had taken on some water and were at least partially diluted. 3. My collection intervals were longer than Holopainen's (1992) (two weeks versus one week), perhaps extending beyond the period of highest attraction to invertebrates for ethylene glycol. 4. There is probably

significant difference in regional ambient conditions between my study and others. The study site presented here was a high elevation forest of spruce and subalpine fir, and during the study unusually cold and wet conditions prevailed, even for that area. Volatility of any compound could be expected to be comparatively low under such conditions.

The gastropod problem.

Gastropods were a significant problem for pitfall trapping. Gastropod independence toward trap or fluid treatments indicates that the group is simply abundant in the surface stratum of this locality, and it will likely occur abundantly in future trapping efforts. Preventative measures may be desirable to reduce slug catches and contamination of samples. Gastropods are often found travelling downward along the vertical surface of trap walls. From this it seems likely that some barrier along the inner surface of the trap might be used as a repellent. Cupreous barriers restricting the passage of terrestrial gastropods are available commercially (Snail Barr™, Custom Copper, Ventura, CA., USA) and have been shown to be reliable, even under rainy conditions (Koehler and Barclay 1983; Moens *et al.* 1967).

Vertebrate disturbance and entrance into traps.

Large vertebrate encounters with traps were independent of collection fluid. I suggest that the concentration of ethylene glycol under operational placement of traps, as from the studies in my wider work, is insufficient to attract large vertebrates. During the trial, small vertebrates were either incapable of differentiating between fluids in traps, or were

indifferent. The open top of the Barber (1931) design is a hazard to small vertebrates, which if captured will compromise the quality of other specimens. The restricted entrances into the Nordlander (1987) design are clearly superior in this regard.

No studies have been done to test the attractive nature of ethylene glycol to non-domestic vertebrates. Its appeal to domestic vertebrates is disputed (Hall 1991; Marshall and Doty 1990), and my data suggest that its use does not further the incidence of disturbance by wild animals. This conclusion applies to the spacing at which my traps were placed (see Chapter 3) and may not be appropriate for other trap configurations.

However, encounters between traps and vertebrates *will* occur at a low frequency and ethylene glycol is a potential hazard in such cases. The Nordlander (1987) design is unique in its integration of trap and lid, and I think will prevent any but the most dextrous animals from obtaining trap contents before upsetting the trap, causing the contents to drain into the soil. Effects of prolonged toxicity in the soil should be investigated for this and alternative preservatives.

Propylene glycol is now being used as an alternative preservative to ethylene glycol, as it has a reduced toxicity for vertebrates (Mochida and Gomyoda 1987), and its preservative qualities for invertebrates are thought to be equivalent to antifreeze-based ethylene glycol (anonymous discussion from the Internet). Its ingestion however, can still be fatal (Dorman and Haschek 1991) and it has been demonstrated to be equally as attractive as ethylene glycol based-antifreeze when presented to gastric-cannulated dogs deprived of

food and water (Marshall and Doty 1990). Propylene glycol is available as antifreeze for specialized recreational vehicles (like snowmobiles and all-terrain vehicles). The increasing use of these vehicles is making this form of antifreeze cheaper than ethylene-glycol based antifreezes, and availability is hence increasing in temperate regions of North America.

Conclusions

My data support the continued use of the Nordlander (1987) trap design. I could demonstrate only minor or inconstant catch differences for ground beetles, when compared with a standard, open-topped trap design. Such differences would have minor consequence for assemblage-level conclusions in ecological studies, and one must accept that any trap design will have some inherent bias with respect to study populations.

Logistical benefits from the Nordlander (1987) design include ease of transport, storage and implementation, as well as protection from changes in fluid concentrations from ambient conditions. Restricted entrance area and access to fluid contents mitigate impacts toward small and large vertebrate animals, respectively. Only the smallest vertebrates can enter the trap. These factors, together with the minor capital investment required to produce the Nordlander (1987) design, should promote its use.

Ethylene glycol is a convenient and inexpensive preservative, suitable especially for large studies requiring extended collection intervals. The precise bias incurred by its use appears to be variable but acceptably limited (and non-existent in this study). In conjunction with a trap design like that from Nordlander (1987), effects toward vertebrate

animals will be negligible. Propylene glycol may be a less toxic alternative but its possible biases toward the capture of invertebrates will need to be tested.

Bibliography

Adis, J., and E. Kramer. 1975. Formadlehyde-Lösung attrahiert *Carabus problematicus* (Coleoptera Carabidae). *Entomologica Germanica* 2: 121-25.

Adis, J. 1979. Problems of interpreting arthropod sampling with pitfall traps. *Zoologischer Anzeiger* 202: 177-84.

Baars, M. A. 1979. Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia* 41: 25-46.

Barber, H. S. 1931. Traps for cave-inhabiting insects. *J. Elisha Mitchell Sci. Soc.* 46: 259-66.

Basedow, T. 1976. Untersuchungen uber das vorkommend der Laufkafer (Col: Carabidae) auf Europadsichen Getreidefeldern. *Entomophaga* 21: 59-72.

Bostanian, N. J., G. Boivin, and H. Goulet. 1983. Ramp pitfall trap. *Journ. Econ. Entomol.* 76: 1473-75.

Bray, J. R., and C. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27: 325-49.

Craig, K. G. 1995. Variation in Carabid Community Structure Associated with Coastal Douglas-fir Forest Successional Stages. M.Sc. Thesis, University of British Columbia, Dept. Zool. Vancouver, British Columbia.

Dorman, D. C., and W. Haschek. 1991. Fatal propylene glycol toxicosis in a horse. *J. Am. Vet. Med. Ass.*. 198: 1643-44.

Fichter, E. 1941. Apparatus for the comparison of soil surface arthropod populations. *Ecology* 22: 338-39.

Greenslade, P., and P. J. M. Greenslade. 1971. The use of baits and preservatives in pitfall traps. *J. Aust. Ent. Soc.* 10: 253-60.

Hall, D. W. 1991. The environmental hazard of ethylene glycol in insect pit-fall traps. *Coleopt. Bull.* 45 (2): 193-94.

Helenius, J. 1990. Effect of epigael predators on infestation by the aphid *Rhopalosiphum padi* and on grain yield of oats in monocrops and mixed intercrops. *Entomologica Experimentalis Applicata* 54: 225-36.

Hertz, M. 1927. Huomioita petokuoriaisten olinpaikoista. *Luonnon Ystävä* 31: 218-22.

Holopainen, J. K. 1990. Influence of ethylene glycol on the numbers of carabids and other soil arthropods caught in pitfall traps. pp. 339-41 *in*: Stork, N. E., ed. *The Role of Ground Beetles in Ecological and Environmental Studies.* London: Intercept.

Holopainen, J. K. 1992. Catch and sex ratio of Carabidae. *Pedobiologia* 36: 257-61.

Holopainen, J. K., and A. L. Varis. 1986. Effects of mechanical barrier and formalin preservative on pitfall trap catches of carabid beetles (Coleoptera: Carabidae) in arable fields. *J. Appl. Ent.* 102: 440-445.

Honek, A. 1988. The effect of crop density and microclimate on pitfall trap catches of Carabidae, Staphylinidae (Coleoptera), and Lycosidae (Araneae) in cereal fields. *Pedobiologia* 32: 233-42.

Kharboutli, M. S., and T. P. Mack. 1991. Realtive and seasonal abundance of predaceous arthropods in Alabama peanut fields as indexed by pitfall traps. *J. Econ. Ent.* 84: 1015-23.

Koehler, C., and W. Barclay. 1983. Snail Barriers. *Calif. Agr.* 37: 11-12.

Lindroth, Carl. H. 1961-1969. *The Ground-Beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska*. (Suppl.) 20 (1961), 24 (1963), 29 (1966), 33 (1968), 34 (1969), & 35 (1969). Lund University, Sweden: Opuscula Entomologica.

Luff, M. L. 1968. Some effects of formalin on the numbers of Coleoptera caught in pitfall traps. *Ent. Monthly Mag.* 104: 115-16.

Luff, M. L. 1975. Some features influencing the efficiency of pitfall traps. *Oecologia* 19: 345-57.

Macfayden, A. 1963. *Animal Ecology. Aims and Methods.* London.

Marshall, D. A., and R. L. Doty. 1990. Taste responses of dogs to ethylene glycol, propylene glycol, and ethylene glycol-based antifreeze. *J. Am. Vet. Med. Ass.*. 12: 1599-602.

Mitchell, B. 1963. Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank). *J. Anim. Ecol.* 32: 377-92.

Mochida, K., and M. Gomyoda. 1987. Toxicity of ethylene glycol, diethylene glycol, and propylene glycol to human cells in culture. *Bull. Environ. Contam. Toxicol.* 38: 151-53.

Moens, R., E. Francois, A. Riga, and W. E. van den Bruel. 1967. A mechanical barrier against terrestrial Gasteropods. *Association Pour Les Etudes Er Recherches De Zoologie Appliquee Er De Phytopatho* 23: 22-27.

Morrill, W. L., D. G. Lester, and A. E. Wrona. 1990. Factors affecting efficacy of pitfall traps for beetles (Coleoptera: Carabidae and Tenebrionidae). *J. Ent. Sci.* 25 (2): 284-93.

Niemelä, J., Y. Haila, E. Ranta, J. Tianen, K. Vepsäläinen, and S. Ås. 1987. Distribution of carabid beetles in four boreal archipelagoes. *Ann. Zool. Fenn.* 24: 89-100.

Niemelä, J., J. R. Spence, and D. H. Spence. 1992. Habitat associations and seasonal activity of ground-beetles (Coleoptera, Carabidae) in central Alberta. *Can. Ent.* 124: 521-40.

Nordlander, G. 1987. A method for trapping *Hylobius abietis* (L.) with a standardized bait and its potential for forecasting seedling damage. *Scand. J. For. Res.* 2: 199-213.

Petruska, F. 1969. On the possibility of escape of the various components of the epigeic fauna of the fields from the pitfall traps containing formalin (Coleoptera). *Acta Universitatis Palackianae Olomucensis Facultas Rerum Naturalium* 31: 99-124.

Pielou, C. 1984. *The Interpretation of Ecological Data*. Toronto: John Wiley & Sons.

Southwood, T. R. E. 1978. *Ecological Methods - With particular reference to the study of insect populations*. London, UK: Chapman & Hall.

Spence, J. R., and J. K. Niemela. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. *Can. Ent.* 126 : 881-94.

Systat Corporation. 1997. *Systat 7 for Windows*. Chicago: SPSS Inc.

Thiele, H. U. 1977. *Carabid Beetles in their Environments*. Berlin: Springer-Verlag.

Van den Berghe, E. 1992. On pitfall trapping invertebrates. *Ent. News* 103 (4): 149-56.

Waage, B. E. 1985. Trapping efficiency of carabid beetles in glass and plastic pitfall traps containing different solutions. *Fauna Norv. Ser. B* 32: 33-36.

Zar, J. H. 1984. *Biostatistical Analysis*. Englewood Cliffs, N.J. USA: Prentice-Hall, Inc.

Chapter 2. Small-scale habitat variation as described by Biogeoclimatic Ecosystem Classification, and its relationship to ground beetle assemblages.

Abstract

Carabid beetles captured by pitfall trapping were used to predict classification of "site-series" (localized) habitats near Smithers, British Columbia. Species assemblages from two seasons of trapping, 1995 and 1996, were compared among four common "site series" habitat classifications found in mature forest and forest remnants. Of eight common species, only one, *Calathus advena* Lec., was trapped in significantly higher numbers in the wet 09 site series. Cluster analysis of species assemblages, using Bray-Curtis index of percent similarity, showed consistent patterns of clustering between years. Clustering patterns were reminiscent of the ordination of those same site types in an edatopic grid, based on soil moisture and soil nutrient regimes. It is suggested that site series is a good foundation for understanding the variation of carabid assemblages, but other important habitat features like woody debris, which are not incorporated in the classification, may be important in refining predictions.

Introduction

Two prominent applications follow from the understanding of natural biotic variation. First, conservation programs may be effectively designed for preserving natural ranges of variation (Niemelä *et al.* 1996; Wilson and Willis 1975). For example, newly implemented forest harvesting approaches, which leave behind various components of pre-harvest stands, are intended to promote structural and biotic variability, both spatially and temporally (Coates and Steventon 1995; CCEM 1995). However, current design does not distribute forest patches over small-scale habitat variation. Further, because the correlation between these habitats and the taxa that may be found in them is so poorly understood, patch retention may not be optimally implemented for its intended objectives. That is, the increased effort needed to produce new harvesting designs, or other conservation efforts, may not be contributing to the conservation of native biological organization.

Second, ecological studies are more aptly replicated by considering full ranges of natural variation (Bergerud 1988; Hicks 1973; Hurlbert 1984). In order to make inferences about treatments over a broad ecological range, investigators must ensure that this range is incorporated in testing hypotheses. When this has been properly done, the results may be applied to areas designated for conservation, which should include similar ranges of variation included in ecological study. Thus, this second factor may have important consequences for the first.

"Natural variability" is a very broad concept (Kouki 1994), but crucial for understanding natural systems (Addicott et. al 1987; Hengeveld 1987; Whittaker and Levin 1977). Systematic descriptions of natural variation have been sought on a largely floristic and physiognomic basis (Barnes 1986; Krajina 1965; Meidinger and Pojar 1991; Pfister and Arno 1980). The British Columbia Biogeoclimatic Ecosystem Classification (BEC) uses a hierarchical approach to describe the distribution of ecosystems within British Columbia (Meidinger and Pojar 1991). Because BEC has been adopted by a majority of BC professionals working in natural resources management, it provides a consistent framework for comparative works describing ecosystem variation. BEC integrates relevant and convenient factors, and stresses the ecosystem as the fundamental unit in biotic management (Meidinger and Pojar 1991). It is commonly used to assign site-specific prescriptions for harvesting and silviculture, some of which consider the conservation of "wildlife" (Banner *et al.* 1993).

This aspect of the system is limited by knowledge regarding the co-occurrence of BEC habitats with taxa other than plants. Do other organisms like invertebrates, fungi or ungulates exhibit hierarchical organizations that may be correlated with those of BEC? If so, then BEC may be used to design conservation areas and to study ecological responses of target groups, say to the effects of anthropogenic disturbances like forest harvesting. The issue is unclear because BEC relies primarily on physiognomic features to define the potential climactic ecosystem, with a secondary reference to plant communities, because they are variable within defined habitat classifications (Banner *et al.* 1993). If plant

communities are only loosely bound to BEC classifications, animal communities may exhibit even less binding.

The co-variation of habitats with particular taxa has been used as a reference to describe communities as fine- or coarse-grained, *i.e.*, varying at finer or grosser scales than the systems they inhabit (Addicott *et al.* 1987; Whittaker and Levin 1977). "Site series" is the finest scale for which BEC resolves ecosystems. Determining a site series requires a description of the higher classification levels for the site region, and the surveying of a plot, 20m x 20m, to include vegetation strata, species presence and percent covers, land form, and soil type. The BEC classifications describe hypothetical vegetation climaxes, given that systems are free from large-scale disturbance for a requisite period. That is, given an area's soils, topography, and climatic regime, the plant assemblage that will eventually occur there is predictable. Figure 4 shows a hypothetical landscape profile with typical site series distributions. Each site series tends toward certain relative abundances of overstorey tree species. Appendix II lists floristic and soil properties of common site series found in high elevation forests near Smithers, BC.

For site series, such "taxon" relationships have been tested by several authors. Distribution patterns of large (Banner *et al.* 1985; Cichowski and Banner 1993), medium (Lofroth 1993) and small mammals (Steventon and Davis 1994) have been shown to be non-random and conspicuously associated with certain site series classifications. For larger animals, certain behaviours, like feeding and denning, may occur in specific habitat

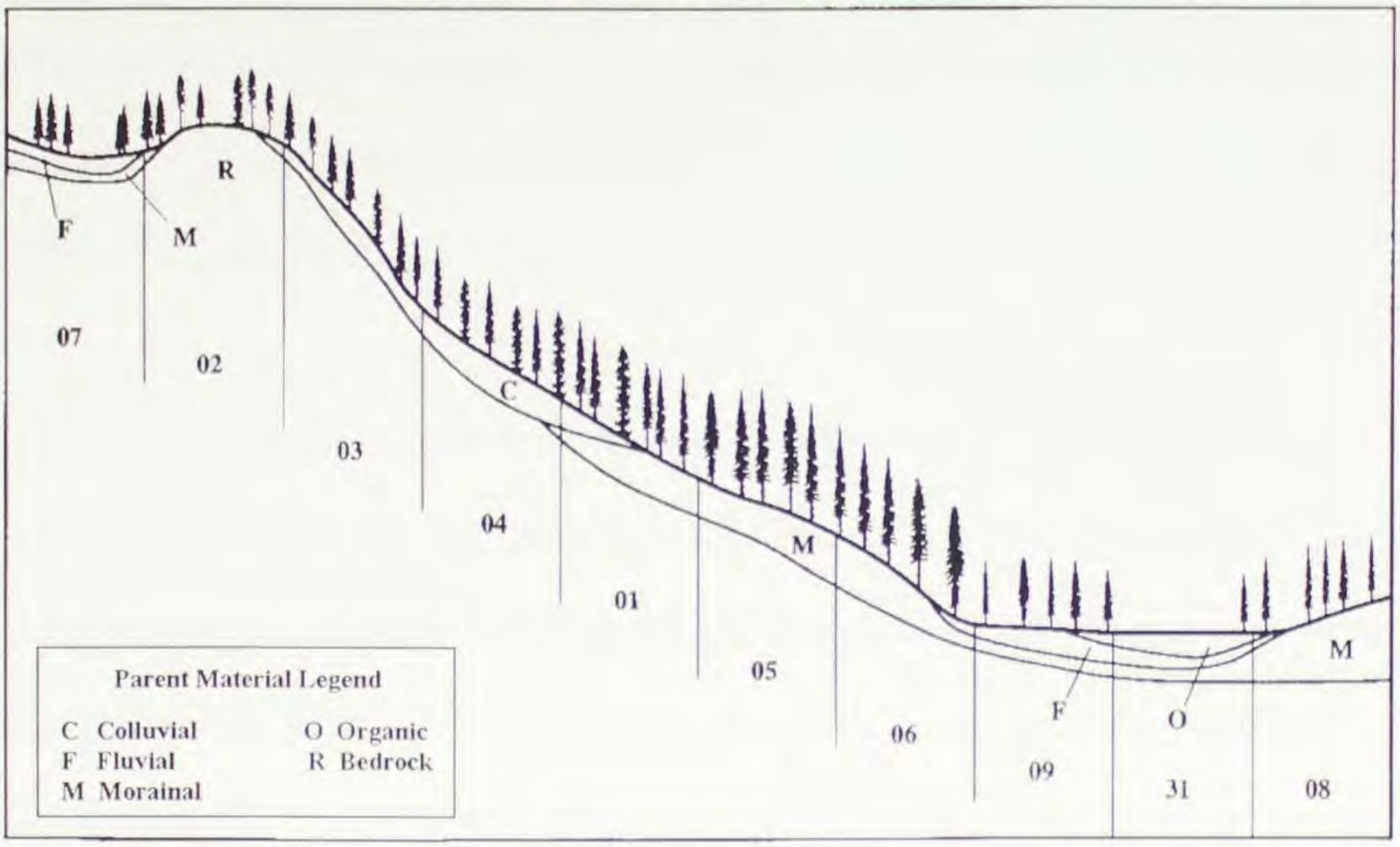

Figure 4. Landscape profile for the Engelmann Spruce-Subalpine Fir Biogeoclimatic subzone, located near Smithers, BC. Numerical references are toward the site series classifications listed in Appendixes I and II (adapted from Banner *et al.* 1993).

types, which are delineated by the localized site series classification of BEC. A loose relationship between BEC site series habitat and terrestrial vertebrates has emerged from these studies. Determining specific habitat needs has been problematic, compounded by the nomadic nature of the animals in question (Banner *et al.* 1985; Cichowski and Banner 1993; Lofroth 1993; Steventon and Davis 1994). No studies using BEC classification have occurred for invertebrates.

Based on range capabilities, smaller animals like arthropods might be expected to demonstrate more significant associations with site series than vertebrates, or at least

have assemblage mosaics that are finer grained. For ground beetles, which are often flightless, this is an especially attractive concept. Relationships with environmental factors like soil form, soil moisture, and plant species, have been reported for ground beetle species and communities (Lindroth 1961-69; Niemelä and Spence 1994; Rykken *et al.* 1997; Walsh *et al.* 1993).

However, underlying mechanisms are unclear and relationships may not be consistent between regions (Niemelä and Spence 1994). Maintaining habitat diversity at a scale of 10-15m has been recommended for maintaining assemblage-level variation for carabid beetles (Niemelä *et al.* 1996). Attempts to explain such spatial variation of forest mycetophilids (Okland 1996), ants (Punttila *et al.* 1991), and carabid beetles (Niemelä and Spence 1994) by association to plant communities, have been only partially successful. Only Rykken *et al.* (1997) have used a hierarchical ecosystem classification like BEC, having then observed little correlation between ecological classification and carabid beetle distributions.

This chapter examines species abundance and assemblage composition of carabid beetles from a range of proximal BEC site series classifications existing as habitats with intact forest canopy: either undisturbed mature forest, forest at stand edges, or in forest left in patches of patch retention harvesting. The objective was to determine whether BEC site series classification could be used as a significant predictor of variation in beetle assemblages. With the widespread use of BEC, the results of this query will be especially relevant for conservation and ecological programs involving terrestrial invertebrates of British Columbia.

Methods and Materials

Data plots (Banner *et al.* 1993) were established in all of the forested plots used otherwise for the general method of study (see chapter 3 for a thorough account of experimental design). Six areas surrounding clearcut and patch retention harvests were studied. Sites in undisturbed forest, areas of canopy cover around the edges of harvests and patches in patch retention harvests were surveyed for understorey plant species composition and percent cover in a 20 x 20m area surrounding trap clusters. Site series determinations were made on the basis of soil nutrient and soil moisture regimes, soil type, land forms, and vegetative communities.

The following limitations occurred in data analysis:

- Only forested plots were used to test hypotheses. Harvested sites could not accurately be described with BEC as vegetation and upper soil strata were frequently disturbed. BEC requires the use of undisturbed properties to properly determine site series (Banner *et al.* 1993)
- "Edge" and "Patch" plots (see Chapter 3) occur in the analysis because site series classifications in these areas could still be accurately determined after disturbance, and because the number of plots I was capable of establishing in undisturbed forest was insufficient to carry out an analysis exclusive of these edge and patch plots.
- The 06 site series was encountered three times, once in transition to a 09 classification. Because it occurred only twice, the 06 series was allocated to the 09

classification, to which it is closely allied (Banner *et al.* 1993). A single classification of 07 was encountered and pooled with the allied 05 Series (Banner *et al.* 1993).

Each site series plot contained a group of five pitfall traps, collected at intervals of two to four weeks throughout the snow-free periods of 1995 and 1996 (June-September).

Identifications were made for all species of Carabidae, using Lindroth (1961-69), and with the generous assistance of Dr. G.E. Ball[3], and Mr. Danny Shepley[4]. Catches at each site were counted as the sum of all five pitfall traps, pooled across all collection dates. Because some traps were disturbed, catches between sites were standardized by dividing catch with number of trap days specific to each site. A single trap operating for a twenty-four hour period completed one trap day.

To improve normality and to ensure that homogeneity of variance existed between treatment populations, a log transformation of the data was performed (Zar 1984). Homogeneity was tested using a Levine test (Systat 1997). One-way ANOVA (Zar 1984), using Systat™ (1997), was used to test the null hypothesis of equal species abundance between site series categories. TUKEY post-hoc multiple comparisons tests were used to discern between individual sample means when a significant ($\alpha <= 0.05$) ANOVA test result was observed. Analysis included Forest, Edge and Patch plots. Since Patch and Edge plots were possibly influenced by edge effects from harvesting, a separate ANOVA analysis was performed, using only Forest plots.

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In cases where there were statistically significant inconsistencies between sampling seasons, 1996 data were partitioned to approximate the collecting period used to generate results from 1995 (since 1995 sampling periods were relatively truncated). ANOVA, as described above, was applied to both data sets to see if consistency could be observed.

As a measure of assemblage similarity, the Bray-Curtis index of percent similarity (Bray and Curtis 1957) was calculated, by hand, for each site series, and used to produce a dendrogram *via* average-linkage cluster analysis (Pielou 1984). The Bray-Curtis index is detailed in Chapter 1. Calculations were made separately for 1995 and 1996 sampling seasons.

Alpha diversity (Southwood 1978) was calculated for all site series and both years using both the Shannon-Wiener and Simpson-Yule diversity indexes (Southwood 1978). Indexes were compared among site series using a Kruskal Wallis non-parametric ANOVA (Zar 1984), using Systat™ (Systat 1997).

Results

Sampling frequency of site series, by treatment type, is given in Table 2. Appendix I provides site series determinations for all trapping locations. Textual descriptions of site series are given in Appendix II. The higher frequencies of Forest plots occur due to their relative frequency in the sampling design (see methods and materials, Chapter 3).

Table 2. Distribution of sampling plots by treatment and BEC site series classification for British Columbia.

TREATMENT	BEC SITE SERIES				
	01	**03**	**05**	**06/09**	**TOTAL**
PATCH	4	5	2	2	**13**
EDGE	4	4	4	0	**12**
FOREST	6	10	5	3	**24**
TOTAL	**14**	**19**	**11**	**5**	**49**

Twenty-eight species of Carabidae were caught over both years. Eight of these were numerous enough for analysis by ANOVA (Table 3). Only *Calathus advena* Lec. had significantly different catches, in the 09 site series. For many species, p-values were <0.20, and the 09 site series frequently exhibited major mean differences from the other series (Table 3).

Data from the Forest plots only showed again that *Calathus advena* Lec. had significantly different catches, in the 09 site series (Table 4). Restricting analysis by collection period to synchronize sampling regimes between seasons did not produce any additional significance in previously inconsistent (between years) results (Table 5). These qualities are reflected in the dendrogram of Bray-Curtis percentage similarity values (Fig. 5). The 09 site series is separated from the others by a wide margin.

Alpha diversity indexes did not discriminate between site series (Table 6). Diversity trends were consistent between years, between site series classifications, and even between indexes.

Table 3. Results of One-way ANOVA testing for site series effect in commonly occurring carabid species near Smithers, BC. Analysis includes plots established in mature, undisturbed forest as well as plots located at stand edges and in small, residual timber patches.[1]

Taxon	1995					1996				
	Mean (catch/site/day) ± SE				ANOVA p-value	Mean (catch/site/day) ± SE				ANOVA p-value
	01	03	05	06/09		01	03	05	06/09	
Bembidion oblongulum Mnh.	0.009 ± 0.005	0.006 ± 0.003	0.004 ± 0.003	0.005 ± 0.005	0.612	0.010 ± 0.003	0.005 ± 0.001	0.015 ± 0.010	0.012 ± 0.007	0.356
Calathus advena Lec.	0.212 ± 0.087	0.206 ± 0.046	0.137 ± 0.107	0.026 ± 0.020	0.333	0.546 ± 0.174**a**	0.241 ± 0.061**a**	0.121 ± 0.079**a**	0.020 ± 0.007**b**	**0.007**
Notiophilus sylvaticus Esch.	----	0.001 ± 0.001	0.001 ± 0.001	----	----	0.016 ± 0.004	0.018 ± 0.006	0.006 ± 0.002	0.002 ± 0.002	0.068
Pterostichus castaneus Dej.	0.010 ± 0.004	0.007 ± 0.003	0.005 ± 0.003	0.014 ± 0.004	0.886	0.014 ± 0.005	0.016 ± 0.002	0.021 ± 0.011	0.025 ± 0.008	0.315
Pterostichus riparius Dej.	0.013 ± 0.010	0.001 ± 0.001	0.008 ± 0.006	0.044 ± 0.031	0.237	0.003 ± 0.002	0.001 ± 0.001	0.013 ± 0.007	0.009 ± 0.005	0.579
Scaphinotus angusticollis Fisch.	0.412 ± 0.075	0.313 ± 0.042	0.568 ± 0.135	0.257 ± 0.070	0.163	0.926 ± 0.121	0.690 ± 0.056	0.641 ± 0.166	0.685 ± 0.201	0.144
Scaphinotus marginatus Fisch.	0.022 ± 0.012	0.014 ± 0.005	0.095 ± 0.033	0.063 ± 0.038	0.252	0.048 ± 0.015	0.034 ± 0.010	0.090 ± 0.038	0.120 ± 0.069	0.112
Trechus chalybeus Dej.	0.011 ± 0.005	0.018 ± 0.008	0.060 ± 0.031	0.148 ± 0.091	0.093	0.021 ± 0.005	0.025 ± 0.006	0.162 ± 0.054	0.083 ± 0.032	0.262
Carabidae	0.691 ± 0.128	0.568 ± 0.073	0.881 ± 0.282	0.573 ± 0.130	0.748	1.588 ± 0.234	1.038 ± 0.112	1.482 ± 0.312	0.877 ± 0.224	0.107

[1]For each row and year, means followed by the same letter were not significantly different (ANOVA (α=0.05) with Tukey post-hoc multiple comparison procedure, Zar (1984)).

Table 4. Results of One-way ANOVA testing for site series effect in commonly occurring carabid species near Smithers, BC. Analysis includes only plots established in mature, undisturbed forest. [1]

Taxon	1995					1996				
	Mean (catch/site/day) ± SE				ANOVA p-value	Mean (catch/site/day) ± SE				ANOVA p-value
	01	03	05	06/09		01	03	05	06/09	
Bembidion oblongulum Mnh.	0.002 ± 0.002	0.002 ± 0.002	----	0.008 ± 0.008	----	0.015 ± 0.005	0.005 ± 0.002	0.003 ± 0.002	0.011 ± 0.011	0.195
Calathus advena Lec.	0.131 ± 0.062	0.169 ± 0.055	0.037 ± 0.016	----	0.121	0.077 ± 0.038**ab**	0.145 ± 0.034**b**	0.041 ± 0.017**ab**	0.026 ± 0.011**a**	**0.016**
Notiophilus sylvaticus Esch.	----	0.002 ± 0.001	0.002 ± 0.002	----	----	0.012 ± 0.004	0.013 ± 0.004	0.011 0.003	----	0.472
Pterostichus castaneus Dej.	0.006 ± 0.003	0.008 ± 0.005	0.004 ± 0.004	0.011 ± 0.006	0.486	0.008 ± 0.004	0.015 ± 0.004	0.003 ± 0.002	0.021 ± 0.005	0.305
Pterostichus riparius Dej.	0.022 ± 0.015	----	0.011 ± 0.009	----	0.337	0.004 ± 0.004	0.001 ± 0.001	0.013 ± 0.010	0.002 ± 0.002	0.820
Scaphinotus angusticollis Fisch.	0.462 ± 0.113	0.350 ± 0.056	0.523 ± 0.061	0.302 ± 0.117	0.271	0.943 ± 0.237	0.592 ± 0.066	0.796 ± 0.131	0.799 ± 0.243	0.430
Scaphinotus marginatus Fisch.	0.036 ± 0.019	0.019 ± 0.006	0.094 ± 0.039	0.068 ± 0.061	0.402	0.072 ± 0.024	0.032 ± 0.007	0.142 ± 0.039	0.154 ± 0.115	0.177
Trechus chalybeus Dej.	0.009 ± 0.007	0.016 ± 0.010	0.030 ± 0.012	0.033 ± 0.010	0.441	0.034 ± 0.008	0.027 ± 0.010	0.058 ± 0.020	0.032 ± 0.002	0.683
Carabidae	0.668± 0.168	0.568 ± 0.096	0.704 ± 0.085	0.423 ± 0.166	0.400	1.169 ± 0.251	0.834 ± 0.088	1.041 ± 0.179	1.051 ± 0.333	0.645

[1]For each row and year, means followed by the same letter were not significantly different (ANOVA (α=0.05) with Tukey post-hoc multiple comparison procedure, Zar (1984)).

Table 5. Results of One-way ANOVA testing for site series effect in *Calathus advena* Lec. Data from 1996 have been omitted for the first collection period (June).

	1995					1996				
	Mean (catch/site/day) ± SE				ANOVA p-value	Mean (catch/site/day) ± SE				ANOVA p-value
	01	03	05	06/09		01	03	05	06/09	
Calathus advena Lec.	0.212 ± 0.087	0.206 ± 0.046	0.137 ± 0.107	0.026 ± 0.020	0.334	0.333 ± 0.121**a**	0.117 ± 0.032**a**	0.198 ± 0.102**a**	0.008 ± 0.003**b**	**0.003**

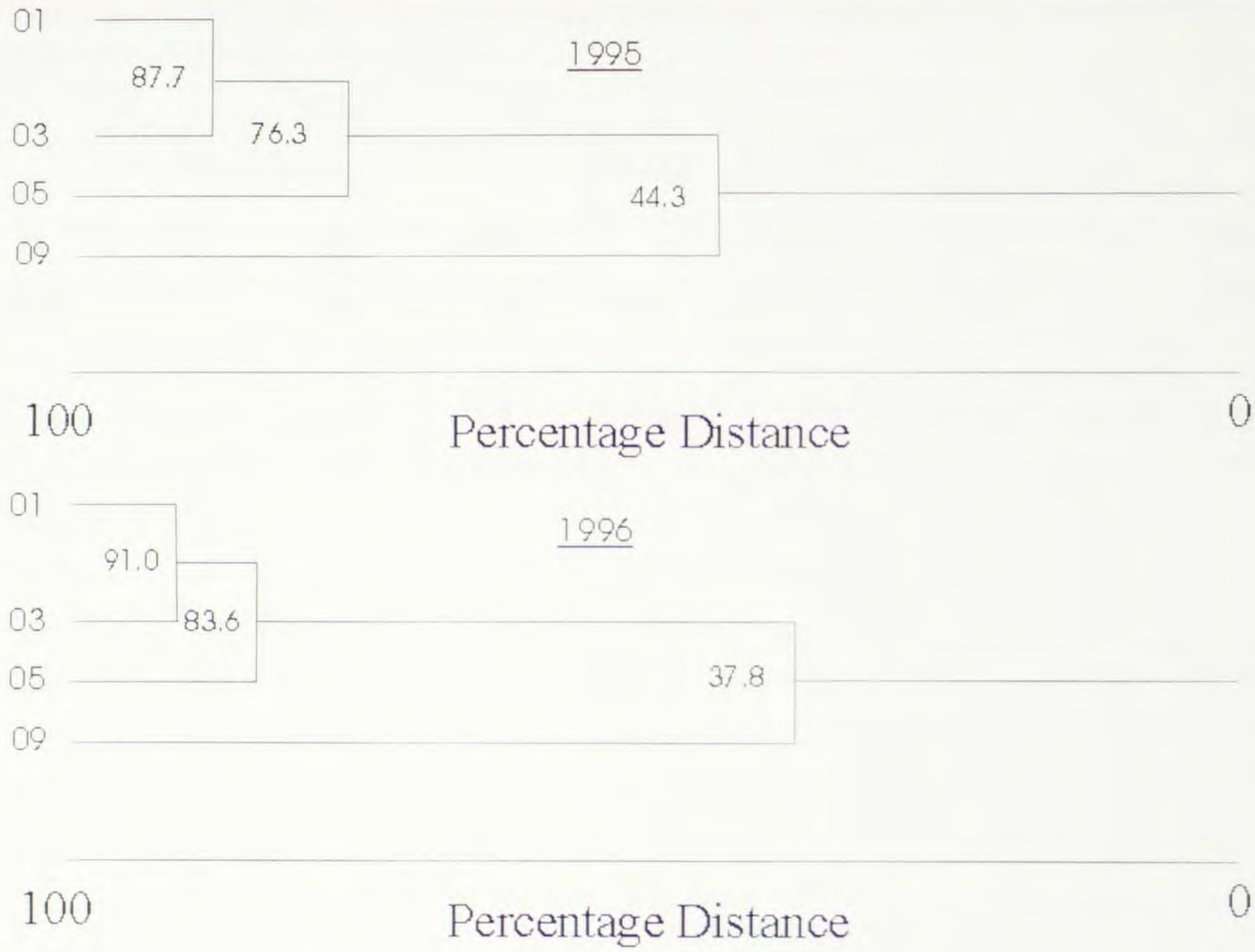

Figure 5. Ordination of site series classifications, by year, based on Bray-Curtis calculations (Bray and Curtis 1957) from carabid pitfall catches, near Smithers, BC.

Table 6. Shannon-Wiener and Simpson diversity indexes used for Kruskal-Wallis ANOVA between BEC site series categories for ground beetles caught near Smithers, BC.

Index	1995					1996				
	Mean Rank				p-value	Mean Rank				p-value
	01	03	05	06/09		01	03	05	06/09	
Shannon-Wiener	32.90	42.70	36.0	20.9	0.836	23.5	33.71	22.91	20.90	0.279
Simpson	23.80	16.33	18.57	18.0	0.402	27.93	30.66	20.55	25.50	0.772

Discussion

Species comparisons.

Habitat has been argued as the primary determinant of life histories for individual species (Southwood 1977, 1988). This referral to environment vs. other important concepts like competition (Connel 1975) has been corroborated for ground beetles in boreal and sub-boreal forests (Niemelä and Spence 1994). Under this tenet, strong relationships between habitat type and a species' population structure should be observed. However, the majority of species caught in this study were randomly distributed among BEC habitat classifications, perhaps indicating an exception to this notion, or more likely that BEC is not inventorying the correct habitat attributes for this group. In addition to their occurrence in forested habitats, many of these carabid species were caught frequently in clearcuts (see Chapter 3), supporting the common impression of carabids as ecological generalists (Hengeveld 1980*a*,*b*; Thiele 1977). Any investigation into spatial distributions should be within the context that carabids are a large, successful and diverse group; for the most part this has been accomplished not through restricted affinities or specializations, but through flexibility. Carabids should be expected not to adhere tightly to habitat classifications. However, several of the species in both years showed p-values lower than 0.20. The possibility of a type II error should be recognized for *Notiophilus sylvaticus* Esch., *Scaphinotus marginatus* Fisch., *Scaphinotus angusticollis* Fisch., *Trechus chalybeus* Dej., and for Carabidae as a whole.

The truncation of the data set to include forested plots was inconsequential, producing random changes in p-values and replicating the difference which *C. advena* had shown in

Table 3. Had there been a general increase in p-values observed with this manipulation, the conclusion would have been that the effects of patch and edge habitats were obstructing patterns otherwise present for site series data.

Between-year variation in responses of *C. advena* could have been a result of the 1995 truncated sampling season, and may indicate that frequency activities of beetles shift (among habitat types) in a mosaic-like fashion throughout the season; *i.e.*, preferred habitat qualities may be seasonally specific. The study site was high elevation (1000 m), and may have characteristic melt and water-availability attributes, especially in very wet sites like a 09 site series. With the very reduced growing season at this location, even slight delays in resource availability (habitats covered with snowpack for example) would comprise net productivity of the beetles for that season. Sota (1986) has detailed a similar phenomenon where, due to shorter summer seasons, altitudinal gradient was correlated with compensatory life-history variation for the carabid *Leptocarabus kumagaii*. However, the Bray-Curtis analysis would refute this, as there was strong consistency in similarity dendrograms between years, despite differences in sampling lengths. Interseasonal shifts in abundance between site series would presumably mask the ability of this type of analysis to discriminate clusters in such consistent order. However, the analysis in Table 5, in which I tried to match sampling regimes between seasons, did not produce any change in the response of *C. advena*, leading to the conclusion that neither sampling period nor edge-related disturbances will alter the results of comparisons among site series.

Otherwise, seasonal activity patterns of species could be responsible for large discrepancies in mean catch and ANOVA p-value, between seasons. Temperate forest carabids have long been known to show bimodal activity peaks in a single season (Thiele 1977), and the truncation of a sampling season could dramatically alter total catches.

Assemblage considerations.

Despite the year to year differences of species responses, the agreement between those and the Bray-Curtis dendrogram in distinguishing the 06/09 series is evocative. The Bray-Curtis dendrogram is indiscriminate of probability distributions and considers the sum *comparative* contribution of all species to categorical comparisons. The wetter, richer and floristically unique 06/09 series harbours a unique carabid assemblage although no species occur exclusively there. Furthermore, carabid-based ordination for site series that the dendrogram produced is reflective of the edatopic grid used to map site series along soil nutrient and moisture regimes (Fig. 6). Soil moisture has been implicated as an important factor in the reproduction of *P. adstrictus* (Goulet 1974). Moisture has been implicated in coarser habitat divisions (Sustek 1994) and identified as an important variable of preference for several carabid species (Thiele 1977). The soil nutrient factor is correlated with changes in litter-layer structure (Banner *et al.* 1993) which, for ground-dwelling assemblages, may contain many determinant qualities, including food and shelter attributes.

In fact, soil form is frequently listed as an important incidental factor in the localized distributions of North American carabids (Lindroth 1961-69). A similar comparison in

Niemelä *et al.* (1992), based on soil moisture only, did not support this as a determinant of carabid assemblages. Data presented here is only suggestive of this relationship. Based on incidental and empirical observations, it is an environmental factor that is worth future investigation.

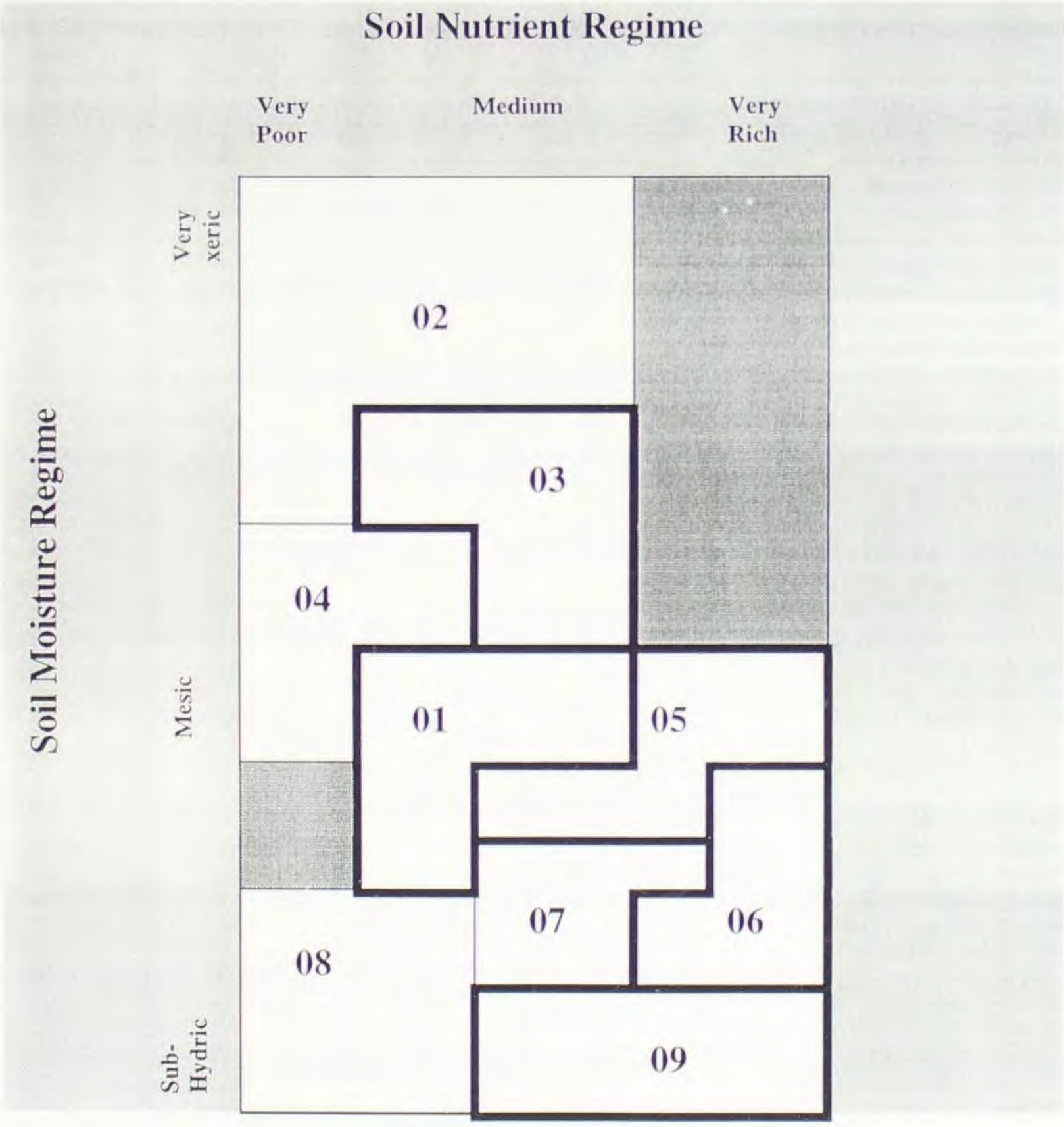

Figure 6. Ordination of site series for the ESSFwv, based on soil nutrients and moisture, adapted from Banner *et al.* (1993). Series outlined in bold are those that occurred in the study.

The 09 series is water-saturated, occurring often in riparian areas and poorly drained depressions (Banner *et al.* 1993). Dichotomies similar to that between other site series

and the 09 have been observed in central Europe. Sustek (1994) observed a similar division when ordinating carabid assemblages between lowland and upland sites in floodplain forests of that area.

Within group variability was considerable, as evidenced by the p-values for individual species. One explanation for this incorporates the concept of a "core binding" of species to BEC habitats with some variation in catches occurring from the "nomadic" tendencies specific to each species. A proximal site series to an 09 for example, could be a contrasting series like an extensive area of xeric 02 (although this extreme is atypical, I have observed it at the study location). The intervening habitat may conceptually span the range of other series, supposed by the application of BEC to occur in between these two series (Banner *et al.* 1993), but occur over such a short spatial scale that typical 09 catches would be heavily influenced by very different 02-type populations.

This concept is built upon the core species concepts proposed by Brown (1984) and discussed in Niemelä and Spence (1994), in which regional faunas are characterized by dominantly abundant species in pitfall catches and accessorized by a more variable component of rarer, satellite species. For the case of the 09 series, several of the core species for this study, notably *S. angusticollis*, and *Trechus chalybeus*, have populations which were suspiciously low, although not meeting the α=0.05 level of significance. Clearly, the regional structure of core species as outlined in Niemelä and Spence (1994) is influenced by small-scale heterogeneity in habitat types. The core-satellite composition is apparent at very localized scales.

Niemelä and Spence (1994) observed the clustering of certain carabid species around individual traps with a few meters' spacing, which they interpreted to be the subtle effects of "microclimate" (light, temperature and moisture). The BEC site series classification is analogous to some intermediate level of a classification of the habitat hierarchy that was used for that study. Their interhabitat comparisons were based on coarser-scale habitats than those that "site series" is intended to describe, and their intertrap comparisons were of a finer scale. In their scales and for the BEC site series, there are hints of hierarchical and predictable organization for carabid beetle assemblages, although variability is not explicable without more detailed autecological studies of the species comprising catches.

The classical error of interpreting pitfall trap catches is to assume a correlation with absolute population density in the area around traps (Adis 1979). It is activity-density that is being measured, although relative activity-densities are a surrogate for absolute population size, assuming that traps are equally efficacious between comparison treatments. At the very least I would say that there is a significant influence by site series type as to the relative efforts particular species are investing in particular habitats, causing an assemblage pattern which is vaguely consistent with BEC site series habitats.

The homogeneity in diversity indexes suggests a consistent equability in forested habitats. The Shannon values are low compared with those reported by Niemelä *et al.* (1992) for lowland forests of central Alberta, perhaps due to the relative elevation of the ESSFwv system, and associated effects on invertebrate assemblages (Mayer and Thayer 1995).

Overall use of BEC.

The hierarchical determination of biotic distributions as proposed for plant communities (BEC, in part) is consistent with characteristics of ground beetle captures (Niemelä and Spence 1994), although plant and animal communities in most cases cannot be precisely predicted from one another.

The hierarchy concept makes intuitive sense: distributions at particular scales are determined by processes of equivalent scale and localized distributions of ground arthropods should be expected to be influenced by localized processes. The key is understanding which environmental factors are responsible. Unfortunately, local-scale factors that govern a highly vagile population (like carabids) as opposed to a sessile one (like plants) are poorly understood. Ground beetles have been characterized not only as generalists, but as nomadic with relatively high rates of travel. Baars (1979) found the carabid species *Calathus melanocephalus* L. and *Pterostichus versicolor* Sturm to have a random walk pattern, covering 66 and 160 m radii in a breeding season, respectively. Loreau and Nolf (1986) describe the mean 'home range' of *Abax ater* Villers as 660 m^2, and Matalin (1994) shows daily flight and walk distances for carabids to be upwards of 200 m and 50 m, respectively. Thus, individuals seem quite capable of extending across site series boundaries within a single breeding season.

I believe that some of the BEC criteria are responsible for a "core-binding" of species to small-scale habitats, as evidenced by patterns like those produced in the Bray-Curtis analyses. In this particular ecosystem, some carabid species' activities were concentrated and diluted predictably in certain habitat regimes. The few studies of species ranges

which exist for carabids indicate that daily and seasonal movement will take them outside of typical BEC site series boundaries.

Lindroth's (1961-69) observations regarding habitat associations of carabid species are only occasionally specific to a certain soil type or equally narrow criterion which might be measured in BEC. This is probably an accurate reflection of specificity patterns for this group as a whole. A few species are tightly bound to habitats, e.g. *Agonum mannerheimii* Dej. (Niemelä *et al.* 1987), but most are less so, as was the case for the species collected here.

My data suggest a coarse-grained response by carabid species and communities to the physio-floristic mosaic termed "site series". This is consistent with conclusions reached by Niemelä *et al.* (1996) and Loreau and Nolf (1986). In a Shannon-Wiener or Simpson-Yule sense there is no variation within the forest mosaic. Site series will be useful in the conservation of some qualities of invertebrate faunas, but might be improved upon. For vertebrates, site series data is supplemented by other habitat characters like coarse woody debris (Steventon and Davis 1994). Determining the additional factors responsible for the distribution of ecologically active groups like the litter fauna may be an important goal in designing forest harvests of the future.

The grain response of the assemblage may change on a regional scale. Niemelä and Spence (1994) have indicated inconsistency between regions as to the local factors distributing a single species. Altitude and latitude are probably major determinants of potential variation in response, in as much as they will affect life history patterns of a

single species (Schatz 1994; Sota 1986). Gereben (1994) found evidence for strong habitat binding in alpine *Nebria* species, based on thermoregulatory activity.

In ecological studies and in the design of conservation efforts, site series will be of moderate effect in ensuring replication of natural variability, as responded to by ground beetles. Variable habitat binding by species, coupled with the gross nature of BEC site series determinations is likely causing the two systems to be imperfectly predicted by one another. When considering site series in the distribution of carabids, special attention should be paid to under- or over-representation of any series type, especially those occurring in extreme ranges of the edatopic grid, as this may cause dramatic alteration to assemblages across the landscape.

Bibliography

Addicott, J. F., J. M. Aho, M. F. Antolin, D. K. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. *Oikos* 49: 340-346.

Adis, J. 1979. Problems of interpreting arthropod sampling with pitfall traps. *Zoologischer Anzeiger* 202: 177-84.

Baars, M. A. 1979. Patterns of movement of radioactive beetles. *Oecologia* 44: 125-40.

Banner, A., W. Mackenzie, S. Haeussler, S. Thomson, J. Pojar, and R. Trowbridge. 1993. *A Field Guide to Site Identification for the Prince Rupert Forest Region.* Land Management Handbook Number 26. BC Min. For. Res. Pgm., Victoria, BC.

Banner, A., J. Pojar, R. Trowbridge, and A. Hamilton. 1985. Grizzly bear habitat in the Kimsquit River Valley, coastal British Coumbia: classification, description, and mapping. pp. 36-49 *in*: *Proceedings-Grizzly Bear Habitat Symposium.* Gen. Tech. Rep., INT-207. Conference Proceedings, April 30-May2US Dept. Ag., For. Ser.

Barnes, B. V. 1986. Varieties of experience in classifying and mapping forestland ecosystems. pp. 5-23 *in*: Wickware, G. W., and W. C. Stevens., eds. *Site Classification in Relation to Forest Management, Symposium Proc.* Conference Proceedings, Aug. 27-29, Sault St. Marie, Ont. Can. For. Serv.

Bergerud, W. 1988. *Understanding replication and pseudo-replication.* Biometrics Information Pamphlet #5. BC Ministry of Forests, Victoria, BC.

Bray, J. R., and C. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27: 325-49.

Brown, J. H. 1984. On the relationship betwen abundance and the distribution of species. *Am. Nat.* 124: 255-79.

CCEM (Cascade Center for Ecosystem Management). 1995. *Residual Trees as Biological Legacies.* Communique 2. CCEM, Corvallis, OR.

Cichowski, D. B., and A. Banner. 1993. *Management Strategy and Options for the Tweedsmuir-Entiako Caribou Winter Range.* Land Management Report No. 83. BC Ministry of Forests, Victoria, BC.

Coates, D. K., and D. J. Steventon. 1995. Patch retention harvesting as a technique for maintaining stand level biodiversity in forests of north central British Columbia. pp. 102-6 *in*: Bamsey, C. R., ed. *Innovative Silvicultural Systems in Boreal Forests.* Conference Proceedings, October 2-8, 1994, Edmonton, AB. Clear Lake Ltd., Edmonton, AB.

Connel, J. H. 1975. Some mechanisms producing structure in natural communities. *in*: Cody, M. L., and J. M. Diamond, eds. *Ecology and Evolution of Communities.* Cambridge, MA: Harvard U. Press.

Gereben, B. A. 1994. Habitat binding and co-existence of carabid beetles in a glacier retreat zone in the Zitteral Alps. pp. 139-44 *in*: Desender, K., M. Dufrêne, M. Loreau, M. L. Luff, and J.-P. Maelfait, eds. *Carabid Beetles: Ecology and Evolution.* Dordrecht, The Netherlands: Kluwer Academic Publishers.

Goulet, H. 1974. Biology and relationships of *Pterostichus adstrictus* Eschsholtz and *Pterostichus pennsylvanicus* LeConte (Coleoptera: Carabidae). *Quaestiones Entomologicae* 10: 3-33.

Hengeveld, R. 1980*a*. Polyphagy, oligophagy and food specialization in ground beetles (Coleoptera, Carabidae). *Neth. J. Zool.* 30 (4): 564-84.

Hengeveld, R. 1980*b*. Qualitative and quantitative aspects of the food of ground beetles (Coleoptera, Carabidae): a review. *Neth. J. Zool.* 30 (4): 555-63.

Hengeveld, R. 1987. Scales of variation: their distinction and ecological importance. *Ann. Zool. Fenn.* 24: 195-202.

Hicks, C. R. 1973. *Fundamental Concepts in the Design of Experiments*. San Francisco: Holt, Reinhart and Winston.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54 (2): 187-211.

Kouki, J. 1994. Biodiversity in the Fennoscandian boreal forests: natural variation and its management. *Ann. Zool. Fenn.* 31 (1): 1-217.

Krajina, V. J. 1965. Biogeoclimatic zones and classification of British Columbia. *Ecol. W. N. Am.* 1: 1-17.

Lindroth, Carl. H. 1961-1969. *The Ground-Beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska*. (Suppl.) 20 (1961), 24 (1963), 29 (1966), 33 (1968), 34 (1969), & 35 (1969). Lund University, Sweden: Opuscula Entomologica.

Lofroth, E. 1993. Scale-dependent Analyses of Habitat Selection by Marten in the Sub-Boreal Spruce Biogoclimatic Zone, British Columbia. M.Sc. Thesis, Simon Fraser University. Burnaby, BC.

Loreau, M., and C. L. Nolf. 1994. Spatial structure and dynamics of a population of *Abax ater*. pp. 165-69 *in*: Desender, K., M. Dufrêne, M. Loreau, M. L. Luff, and J.-P. Maelfait, eds. *Carabid Beetles - Ecology and Evolution*. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Matalin, A. V. 1994. The strategy of dispersal behavior in some Carabidae species of Southeastern Europe. pp. 183-88 *in*: Desender, K., M. Dufrêne, M. Loreau, M. L. Luff, and J.-P. Maelfait, eds. *Carabid Beetles - Ecology and Evolution*. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Mayer, E., and K. Thayer. 1995. Animal Diversity at High Altitudes in the Austrian Alps. pp. 97-110 *in*: Chapin, F. S., and C. Körner, eds. *Arctic and Alpine Biodiversity*. Ecological Studies, 113. NY: Springer-Verlaf.

Meidinger, D., and J. Pojar. 1991. *Ecosystems of British Columbia*. Special Report Series Number 6. BC Ministry of Forests, Victoria, BC.

Niemelä, J., E. Haila, T. Halme, P. Pajunen, P. Puntilla, and H. Tukia. 1987. Habitat preferences and conservation status of *Agonum mannerheimi* Dej. in Häme, southern Finland. *Notulae Entomologicae* 67: 175-79.

Niemelä, J. K., and J. R. Spence. 1994. Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. *Ecography* 17: 166-75.

Niemelä, J., Y. Haila, and P. Puntilla. 1996. The importance of small-scale heterogeneity in boreal forests: varation in diversity in forest-floor invertebrates across the succession gradient. *Ecography* 19: 352-68.

Niemelä, J., J. R. Spence, and D. H. Spence. 1992. Habitat associations and seasonal activity of ground-beetles (Coleoptera, Carabidae) in central Alberta. *Can. Ent.* 124: 521-40.

Okland, B. 1996. Unlogged forests: important sites for preserving the diversity of mycetophilids (Diptera: Sciaroidea). *Biol. Conserv.* 76: 297-310.

Pfister, R. D., and R. F. Arno. 1980. Classifying forest habitat types based on potential climax vegetation. *For. Sci.* 26: 52-70.

Pielou, C. 1984. *The Interpretation of Ecological Data*. Toronto: John Wiley & Sons.

Punttila, P., Y. Haila, T. Pajunen, and H. Tukia. 1991. Colonisation of clearcut forests by ants in the southern Finnish taiga: a quantitative survey. *Oikos* 61: 250-262.

Rykken, J., D. E. Capen, and S. P. Mahabir. 1997. Ground beetles as indicators of land type diversity in the Green Mountains of Vermont. *Conserv. Biol.* 11 (2): 522-30.

Schatz, I. 1994. Life strategy of an alpine carabid; *Pterostichus jurinei* (Coleoptera: Carabidae). pp. 213-17 *in*: Desender, K., M. Dufrêne, M. Loreau, M. L. Luff, and J.-P. Maelfait, eds. *Carabid Beetles: Ecology and Evolution.* Dordrecht, The Netherlands: Kluwer Academic Publishers.

Sota, T. 1986. Carabid populations along an altitudinal gradient: life history variation of *Leptocarabus kumagaii* (Coleoptera: Carabidae). pp. 139- 147 *in*: den Boer, P. J., M. L. Luff, D. Mossakowski, and F. Weber, *Carabid Beetles: Their adaptations and dynamics.* New York: Gustav Fischer.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? *J. Anim. Ecol.* 46: 337-65.

Southwood, T. R. E. 1978. *Ecological Methods - With particular reference to the study of insect populations*. London, UK: Chapman & Hall.

Southwood, T. R. E. 1988. Tactics, strategies and templets. *Oikos* 52: 3-18.

Steventon, J. D., and L. Davis. 1994. *Progress Report: Maintaining Wildlife Diversity in Managed Landscapes: A Test of Site Unit and Seral Stage Mapping to Predict Small Mammal Occurrence in SBS Forests.* BC Forest Service, Forest Sciences Section, Prince Rupert Region, Smithers, BC.

Sustek, Z. 1994. Classificationof the carabid fauna in the floodplain forests in Moravia and Slovakia. pp. 371-76 *in*: Desender, K., M. Dufrêne, M. Loreau, M. L. Luff, and J.-P. Maelfait, eds. *Carabid Beetles: Ecology and Evolution.* Boston: Kluwer Academic.

Systat Corporation. 1997. *Systat 7 for Windows*. Chicago: SPSS Inc.

Thiele, H. U. 1977. *Carabid Beetles in their Environments*. Berlin: Springer-Verlag.

Walsh, P. J., K. R. Day, S. R. Leather, and A. Smith. 1993. The influence of soil type and pine species on the carabid community of a plantation forest with a history of pine beauty moth infestation. *Forestry* 66 (2): 135-45.

Whittaker, R. H., and S. A. Levin. 1977. The role of mosaic phenomena in natural communities. *Theor. Popul. Biol.* 12: 117-39.

Wilson, E. O., and E. O. Willis. 1975. Applied biogeography. pp. 523-34 *in*: Cody, M. L., and J. M. Diamond, ed. *Ecology and Evolution of Communities.* Cambridge, MA: Harvard U. Press.

Zar, J. H. 1984. *Biostatistical Analysis*. Englewood Cliffs, N.J. USA: Prentice-Hall, Inc.

Chapter 3: A Comparison of Ground Beetle Response to Clearcut and Patch Retention Harvesting.

Abstract

The retention of small (0.1-2.0 ha) patches of standing timber in clearcuts, as a method of improving the regeneration of pre-harvest carabid fauna, was investigated relative to conventional clearcutting. Twenty-eight species totaling 15,799 individuals of Carabidae were collected from two seasons of pitfall trapping in north central BC, spanning over 46,000 trap nights. Abundance was dominated by four species comprising 92.4% of the catch. No species could be characterized as "mature-forest specialists", or "forest generalists". The absence of a typical open-habitat specialist fauna, notably the genera *Amara* Bonelli and *Harpalus* Latreille, was noted and explained in the context of disturbance frequency in the surrounding landscape. Other possibilities include regional variation for the response of widespread species to disturbance, and the regional variation of the conditions occurring in the aftermath of clearcutting. Cluster analysis of carabid fauna consistently separated treatments according to intuitive notions of their habitat integrity. Patches and edge habitats immediately inside the forest canopy contained assemblages more closely related to mature forest than cleared areas. Harvested areas with retained patches had carabid assemblage patterns distinct from typical clearcuts, based primarily on changes in abundance of common species. The role of patches in producing this effect is thought to be influenced by the integrity of the surrounding forest matrix and its biota. The role of patch retention harvesting in regenerating pre-harvest biota may be severely reduced or nullified if harvesting in the surrounding landscape is excessive.

Introduction

Ecological succession is a fundamental biotic process (Shuggart 1984). Succession is conceived by ecologists as a cumulative and directional change in species composition of a defined area, over time (Barbour *et al.* 1987). The process provides a strong element of predictability toward the occurrence of either particular species or their ecological equivalents in space and time.

Succession generally follows disturbance, also a fundamental process in natural systems. Disturbances are characterized as discrete events disrupting preexisting biological and physical organization (Pickett and White 1985). Many of these events, like fire and insect outbreaks, occur at predictable average frequencies, and are integral in the composition of the ecosystems in which they occur (Schowalter *et al.* 1981; Pickett and White 1985). Anthropogenic disturbances, however, have been imposed on such radically large scales, and at such frequencies, that fundamental ecosystem processes and associated services (clean air and water, "aesthetics", food, and more) are in many areas endangered (Noss and Cooperrider 1994).

In forest harvesting, *silviculture* has been the operative term for promoting an acceptable fashion of succession after harvest. The operational definition from the BC Government is "...managing forest vegetation by controlling stand establishment, growth, composition, quality and structure, for the full range of forest resource objectives." (BC

MOF/MOE 1995). Literally, *silva* is the Latin for *forest* (Forbes 1996). However, it can be argued that a forest is much more than trees, and that "forest-culture" should strive for the maintenance of entire biota during the process of succession following disturbance.

In its supposed failure to support biotic regeneration, traditional clearcut harvesting has generated much controversy (Hammond 1991). Since the harvest is the initial and most committing step in silviculture, establishing a template from which all ensuing actions must follow, it is a very important component. Hammond (1991) summarizes the criticisms against clearcutting, including the failure of these harvests to mimic natural disturbances like insect outbreaks and wildfire. Wildfires can create vegetation distributions quite different from clearcutting (DeLong and Tanner 1996; Eberhardt and Woodward 1987). Wildfires are more variable in size, distribution, shape and intensity of disturbance than clearcut harvesting. It is a common presumption that these are important and negative differences for the regeneration of the pre-harvest biota. However, for the majority of forest organisms there are scant data to examine this issue.

Insects are important in forests, because of their diversity (Winchester and Ring 1996), abundance (Stork 1987, 1991) and the imposed ecological roles which follow from these qualities (Franklin *et al.* 1989; Schowalter *et al.* 1986; Stork 1987), but like many aspects of terrestrial invertebrate biology, succession for this group has received little attention in the literature. Southwood *et al.* (1979) has given a detailed account of plant/arthropod relationships through succession, indicating that there can exist very perceptible

successions in insect faunas, and that these can be strongly related to taxonomic and architectural succession of concurrent plant communities.

Carabid beetles have been proposed as an indicator group (Eyre *et al.* 1989; Heijerman and Turin 1994; Maelfait and Desender 1990; Mossakowski *et al.* 1990; Pearson and Cassola 1990; Refseth 1980). Some of these authors claim the Carabidae to be highly influenced by environmental parameters and thus efficient indicators of habitat changes. However, no comparative data against other taxa have been given. Apparently these indicator studies have relied on carabids because they are ubiquitous, diverse, easily trapped and relatively well known taxonomically (den Boer 1986), and to a lesser extent ecologically. Alternatively, the predatory nature of the group lends it toward generalist practices (Thiele 1977), and relying on it to represent broader trends for invertebrates may lead to insensitive conclusions, as there are probably more responsive ecological and taxonomic groups. For example, the concurrently collected Staphylinidae are more speciose and, because they include a much wider array of feeding guilds, may be more responsive to habitat modifications (J. Spence[5], pers. comm.).

From the carabid generalist notion, den Boer (1977) has argued that ground beetles should be rigorous recolonizers of disturbed habitat and could assumedly maintain healthy metapopulations under fragmentation pressures. De Vries (1996) has confirmed this ability in *Pterostichus lepidus* with reintroduction experiments. His data show the persistence of a metapopulation in both continuous and discontinuous heathland habitat patches. De Vries and den Boer (1990) showed that fragmentation of habitat to less than

5 ha caused several satellite populations of *Agonum ericeti* to become extinct while larger core populations in habitat blocks of >50 ha had persisted between 24 and 66 years after fragmentation. This is thought to occur because "stable" populations actually undergo periodic extinction, or at least depletion, and are maintained only by the influx of individuals from surrounding source populations. The importance of metapopulation structure appears to be species-specific, but more specific examples will be needed to establish rigorous models. So although there are no specific data to examine the issue, forest species of invertebrates should be assumed to be susceptible to the phenomenon in which there is a cyclical depression of abundance following widespread disturbances. By cyclical I mean that source populations in undisturbed forest interiors become incapable of recolonizing disturbed sites, because they themselves have not received necessary influxes. Metapopulation theory proposes species as having tenable existences, with interconnected populations continually on the verge of either colonization or extinction (Harrison 1993). With an increasing magnitude and/or frequency of disturbance in the forest matrix, populations within undisturbed forest may be reduced to a state where colonization of disturbed sites is barred. Localized population effects may be cumulative over a landscape.

And indeed there are examples for invertebrates that lend support to this notion. Siitonen and Martikainen (1994) give a broad-scale account of saproxylic insects in Finland, indicating a successional component that has been largely eliminated because of intensive forest use. Spence *et al.* (1996) have given an account of carabid beetle succession in a chronosequence of clearcut harvests in central Alberta. Those findings indicated that

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several species might be unable to regenerate in clearcuts, for as long as 27 years following harvest. These studies outline *problems* associated with traditional forest harvesting very well: under intensive forest harvesting, certain elements of forest biota, (insects in these cases) will be eliminated from successional sequences. This may pose a threat of extinction for some species, and radical alterations in insect assemblages across the landscape.

To conserve pre-disturbance states of biological organization, methods of mitigating localized destruction of populations should be sought. One approach to this is to try and emulate natural disturbance regimes. In a general sense, such an approach has been adopted by recent forest harvesting initiatives in BC, designed to mimic more closely the patterns of wildfire (Coates and Steventon 1995). Structural diversity in stands is thought to act as a surrogate for maintaining overall biotic diversity, an approach that has received some initial support from the interpretation of avian responses (Mackenzie and Steventon 1996). In this chapter I compare the carabid fauna from clearcut and patch retention harvests in early (4-7 years) stages of forest regeneration (patch retention is discussed in detail in the Introduction). The intent was to measure initial responses of the fauna and to make inference about the effectiveness of two harvesting systems in promoting carabid succession toward the state from which it was altered. Does patch retention harvesting create different invertebrate patterns than clearcutting? How do these patterns compare with undisturbed communities? In invertebrate terms, what are the higher-order spatial and temporal consequences of practicing one system over the other?

To this end the following hypotheses are offered:

- Carabid species demonstrating dependency upon mature forest (not captured in harvested areas) will be present in patches.
- Patches in patch retention harvesting harbour carabid beetle assemblages equivalent to those found in surrounding, undisturbed forest.
- Harvested areas in patch retention will harbour carabid beetle assemblages that more closely resemble those found in undisturbed forest than do those found in conventional clearcuts.

Methods and Materials

Study area.

Through the summers of 1995 and 1996 modified pitfall traps (Chapter 1) were used to collect Carabidae from three paired replicates of patch retention and clearcut harvests. The study took place in the Copper River Valley, near Smithers, BC (Fig. 7), one of the few areas in BC with patch retention harvests prior to 1995. Study harvests were located in the lower elevations of the Engelmann Spruce-Subalpine Fir biogeoclimatic zone (BGCZ), and the Wet, Very Cold biogeoclimatic subzone (hereafter referred to as the ESSFwv; see Meidinger and Pojar 1991). The ESSF BGCZ is widely distributed at higher elevations throughout the Province (Fig. 8) and is commonly the highest forested system in mountainous and rugged terrain. ESSF typically occurs above Interior Cedar-Hemlock, Montane Spruce, and Sub-Boreal Spruce zones, but is absent in the coastal and northern areas of the Province where other high-elevation systems predominate. Relative to other BGC zones, the ESSF is highly variable in timber production and densities as it

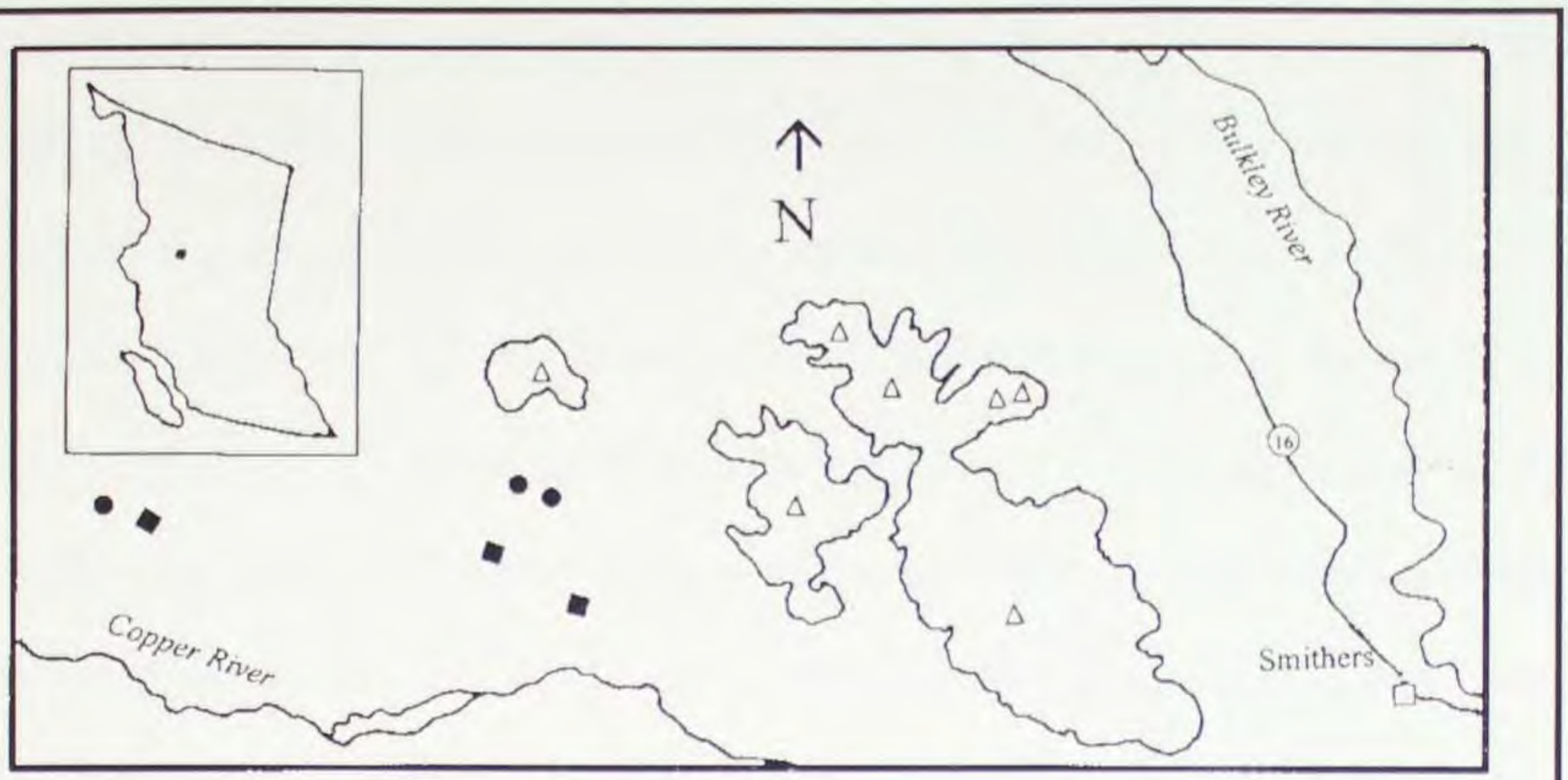

Figure 7. Study area, near Smithers, British Columbia, Canada.

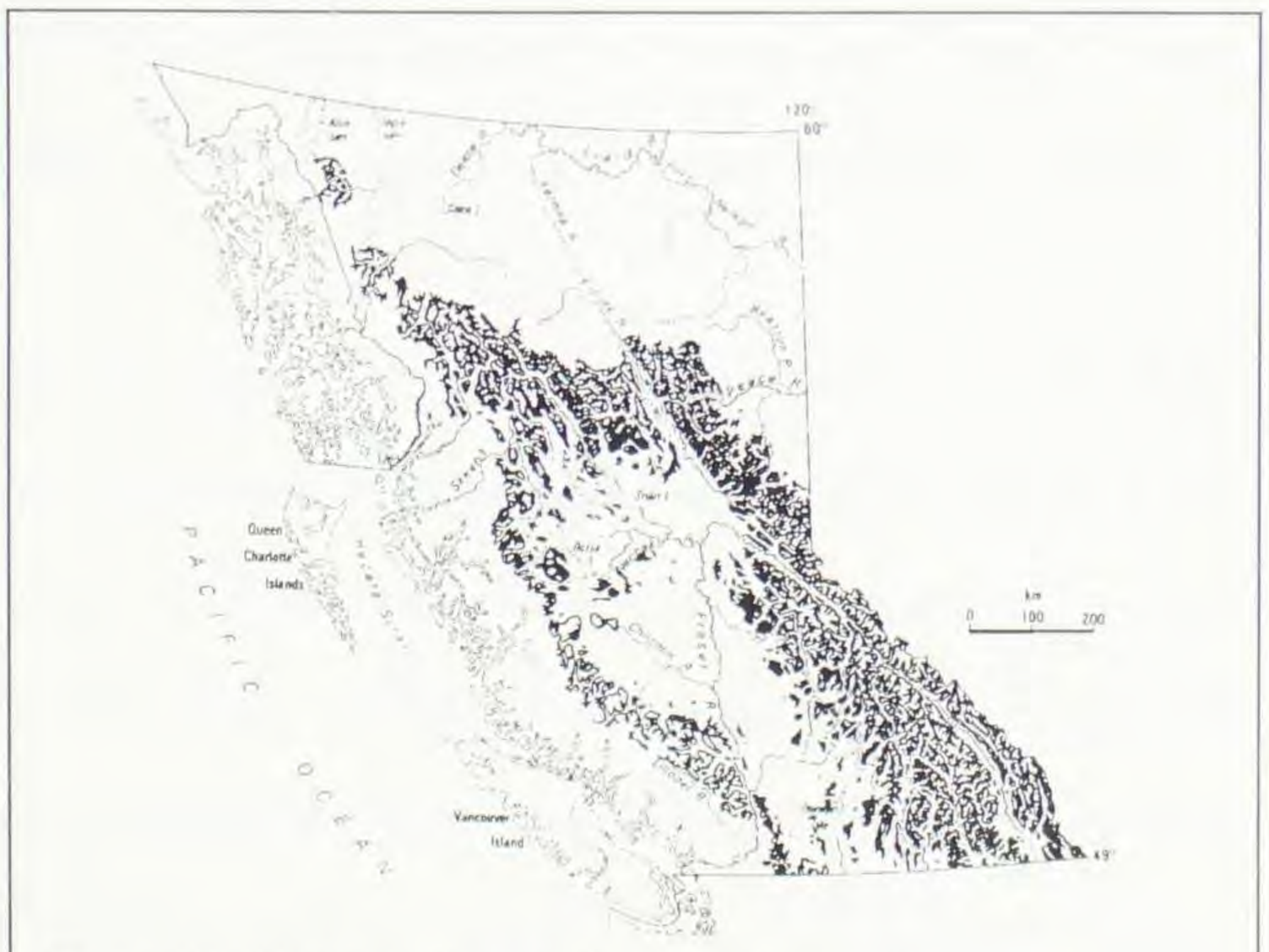

Figure 8. Distribution of the Engelmann Spruce-Subalpine Fir Biogeoclimatic Zone (in black) in British Columbia.

reaches from several hundred meters below tree line, breaking into subalpine parkland near its boundary with Alpine Tundra. The ESSF has a cold and snowy continental climate, ranging from 2000 m maximum elevation in the southern areas of the Province to 1500 m at the northern limit (Farnden 1994). Although there are no summarized data for the wv subzone, northern subzones have mean annual temperatures near 0 °C and maybe two months' or fewer frost-free days (Farnden 1994); only tree species tolerating extended periods of frozen ground will occur there (Mackinnon *et al.* 1992). Overstorey is dominated by Engelmann or white spruce and subalpine fir, with the former living longer and characterizing mature forests. Lodgepole pine is a common seral species in this zone, and both pine and western hemlock can comprise minor stand components (Coupé *et al.* 1991). Recent harvesting increases in these systems may reflect increases in timber values, and resource depletion in more accessible systems; typically the ESSF biogeoclimatic zone has been viewed as a relatively poor system for harvest due to low timber quality and inaccessibility (Doug Steventon[6], pers. comm.). This is changing as timber availability in more accessible and productive regions decreases.

Three replicate patch retention blocks of similar habitat composition were matched with three standard clearcut blocks for pairwise comparison (see Fig. 9). Various stand attributes, acquired from BC Forest Service timber cruise reports, are shown in Table 7. All blocks had been harvested within 24-40 months of first being sampled. Harvests had been priorly hand-felled and line-skidded to landings and roads (soil compaction and mechanical damage to the litter layer are typical effects of this harvest method).

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Pitfall traps were placed in five treatment types: (1) open areas in clearcuts, (2) open areas in patch-retention sites, (3) interior patch habitats in patch retention sites, (4) interior habitats of undisturbed forest adjacent to both types of harvest, and, (5) areas at the edge of patch retention harvests (in 1996 samples only; see below). Figure 9 is a simplified diagram of this design.

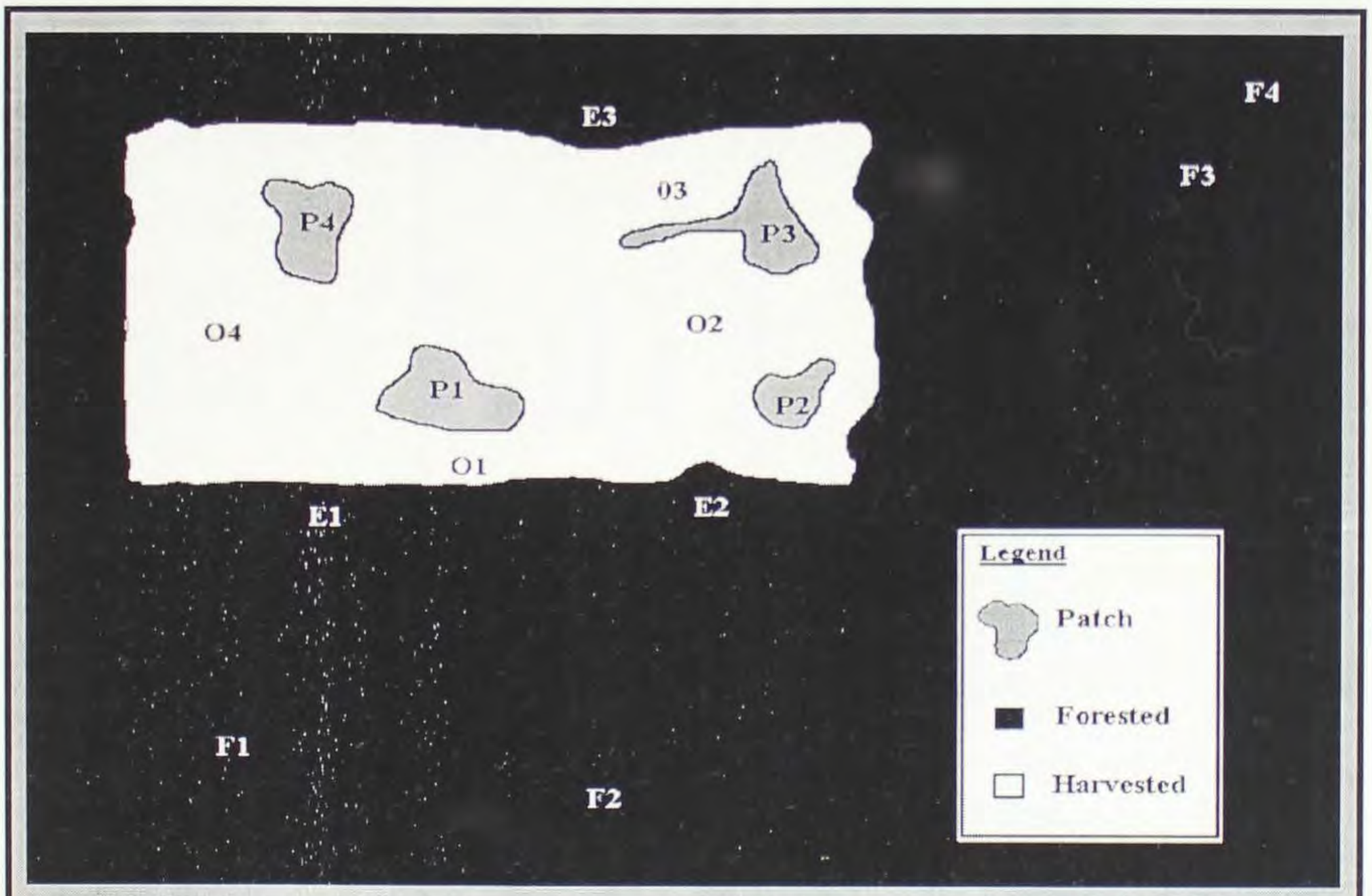

Figure 9. Diagrammatic representation of sampling regime in a "patch retention" harvest. Letters E, F, O and P indicate clusters of pitfall traps, in harvesting treatments as referred to in the text.

Plots consisted of pitfall traps in clusters of five, configured with a central trap and four satellite traps, each at one of the four cardinal directions, and each 5 m from the central trap. Traps were filled with saturated brine in 1995, and ethylene glycol-based antifreeze in 1996. See Chapter 1 for a detailed description of trap construction and collection media.

Table 7. Selected stand attributes of harvested sites studied near Smithers, BC.[1]

Block # (# plots used to create data)	Harvest Type[2]	Number of growing seasons between harvest and first being sampled in this study[3]	Area (ha) of opening including retention	Slope (%) / Aspect	Elev. (m)	Post-harvest Treatments[4]	Average diameter-at-breast-height all species (cm)	% Distribution overstorey conifer spp by volume (Bl/Sx/Pl/Hw)[4]	Density of overstorey, all conifer spp. (stems/ha)
1 (32)	PR	3.5	48	5-25/S-SW	1000	*Plant Pl Sx	28	55/21/23/1	654
2 (30)	CC	3.5	47	14/S-SW	1000	Plant Pl Sx	28	61/24/15/0	674
3 (38)	PR	2.5	45	5-30/N-NW	975	Plant Pl	29	60/24/8/8	656
4 (30)	CC	4	43	19/NE-N	975	Plant Sx Pl	28	58/22/19/1	748
5 (41)	PR	3	41	5-30/ variable	900	Plant Pl Sx Bl	32	72/15/11/2	643
6 (33)	CC	2	49	5-35/S-SW	950	Plant Pl Sx	34	77/11/0/12	659

[1] Compiled from information contained in timber cruises and pre-harvest silviculture prescriptions housed with the Bulkey Forest District Office (BC Ministry of Forests), Smithers, BC. Block numbers refer to individual License numbers as follows: 1=A37574; 2=A31698; 3=A37541; 4=A31699; 5=A36433; 6=A36435.
[2] PR=Patch Retention; CC=Clearcut.
[3] Growing season includes the months of May-October (qualitative judgment based on field observations).
[4] Species codes are as follows: **Bl**, subalpine fir (*Abies lasiocarpa*); **Sx**, hybrid white spruce (*Picea glauca* x *engelmannii*); **Pl,** lodgepole pine (*Pinus contorta* var. *latifolia*); **Hw**, western hemlock (*Thuja plicata*).

Measurements from mature forest were considered a control treatment. In each harvested block there were at least four, occasionally more, sample plots placed randomly within the aforementioned broad habitat classes (mature forest, harvested areas, patch interiors, and forested edge areas in patch retention blocks). The number of appropriate patches occurring in each block limited number of sampling plots per treatment. Sampled patches were chosen by aerial photograph interpretation, focusing on patches exhibiting sufficient size and shape so as to encompass a trap cluster, with at least 10 m of standing forest between any satellite trap in the cluster, and the patch edge. In two cases four plots per block were established, and in the third case, five plots were established.

Collections were made on a bi- or tri-weekly basis over the sampling period June 21-August 18, 1995, and in one-month intervals, June 6-September 13, 1996. During the 1995 collections, traps were implemented asynchronously, as much as a month apart, due to limited available labour. In 1996, all traps were activated within three days of one another, immediately following snow melt in early June.[7] All traps were operated in 1996 until mid-September, at which point catches had become sparse. Table 8 summarizes collection periods among blocks, treatments, and years.

In 1995 collection fluid was strained from the samples with a standard fuel funnel (a plastic funnel with a 3 cm diameter wire mesh screen in the center) into a 4 l container, which at the beginning of each collection contained fresh salt water. In this way

[7] Evidence of the appropriateness of this timing was found in several individuals of *Calathus advena* Lec. (Coleoptera: Carabidae) stuck to the fiber tape used to seal off traps at the end of the previous season; all individuals observed were still alive and had presumably only recently emerged from quiescence.

Table 8. Collection periods for pitfall traps used near Smithers, BC.

Year	Block Number	Start Date	1st Collection	2nd Collection	3rd Collection	Total trapping days
1995	1	28 June	14 July	27 July	16 August	50
	2	7 July	28 July	18 August	--	43
	3	21 June	6 July	26 July	16 August	56
	4	17 July	26 July	16 August	--	31
	5	12 July	27 July	17 August	--	36
	6	12 July	27 July	17 August	--	36
1996	1	6 June	July 6	12 August	13 Sept.	99
	2	6 June	July 5	7 August	12 Sept.	98
	3	6 June	July 5	7 August	12 Sept.	98
	4	7 June	July 6	12 August	13 Sept.	98
	5	7 June	July 7	13 August	14 Sept.	99
	6	7 June	July 6	13 August	14 Sept.	99

sampling fluid was partially refreshed. Brine was completely replaced if it appeared to be unacceptably contaminated as evidenced by sight or smell. Contents were rinsed into individual specimen containers with 70%, denatured ethanol and transported to the laboratory. Pitfall traps were wiped clean of debris and accumulation, refilled with salt water and replaced in the ground. In 1996, with the institution of ethylene glycol as a preservative, the collection and sorting process became more efficient. Samples were strained through cotton medical gauze of two layers' thickness (approx. 10 x 10 cm), and closed with a twist-tie and water-proof label (John Spence[8], pers. comm.). Enough glycol had permeated samples to allow them to remain in this state, unrefrigerated, for lag times as long as a month between sampling and sorting. With this method, pack volume

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needed to remove samples from the field was considerably reduced, as an entire collection (375 traps, one date) could fit into twelve 1 l containers.

The addition of plastic inserts to traps was made in 1996 (Spence and Niemelä 1994). Inserts were 7 cm in height, made from the cut-off bottoms of containers identical to those used in making the original traps. Placing the inserts into pitfall traps allowed the trap-vegetation/soil complex to remain undisturbed during collections; inserts could be removed, emptied and replaced independently of the containing trap (Spence and Niemelä 1994).

Sorting was conducted during periods between collections and during the fall months after each season. Samples were sorted into the following component groups: ground beetles (Coleoptera: Carabidae); rove beetles (Coleoptera: Staphylinidae), spiders (Araneae); mites and springtails (Araneae: Acari / Insecta: Collembola); residuals (all other material). Carabids from 1995 were mounted on pins and stored in Cornell™ drawers. Initial identifications of carabid species required pinned specimens, as each specimen could be moved through successive sorting processes and remain associated with collection information on the pinning label. All other samples, including 1996 carabids, were stored by trap in 10x75 mm borosilicate vials with 70% ethanol. Vials were capped with cotton batting, removing air bubbles, and inverted into a 500 ml glass jar also containing 70% ethanol. Jars were sealed with Parafilm™ and given an identifying label for contents and collection dates. Individual vials and pinned specimens were given either a waterproof/ pencilled label or an archival label of acid-free rag card,

respectively. Each label contained the following information: 1. License number of the harvested area; 2. A letter and number code identifying the trap from which specimen(s) came; 3. Collection period (date); 4. Taxon to which the specimen(s) is/are classified; and 5. Collector's name.

Carabid beetle species determinations were made with a high-quality dissecting microscope, up to 100 X magnification, using external morphological characters, according to Lindroth (1961-1969). A subsample of specimens was kindly reviewed, and determinations confirmed by Dr. George Ball.[9]

Analysis.

Catches at each site were counted as the sum of all five pitfall traps, pooled across all collection dates. Because some traps were disturbed, catches between sites were standardized by dividing catch with number of trap days specific to each site. A single trap operating for a twenty-four hour period equals one trap day.

Data were analyzed using single-factor ANOVA (Zar 1984), using SYSTAT for Windows™ (Systat 1997). When significant differences occurred, TUKEY post-hoc multiple comparisons tests were used to differentiate among treatment means (Zar 1984). To improve normality and to ensure that homogeneity of variance existed between treatment populations, a log transformation of the data was performed (Zar 1984). Homogeneity was tested using a Levine test (Systat 1997). The Bray-Curtis index of percent similarity was calculated by hand, for data pooled by each of the treatment

classes (Bray and Curtis 1957; see Chapter 1). The resulting indexes were subjected to average-linkage cluster analysis, also performed by hand (Pielou 1984).

Results

Overall diversity patterns.

Twenty-eight species in 17 genera were recorded over two seasons of trapping, comprising 46, 451 trap days. Abundance was dominated by four species, comprising 92.4% of the catch (Table 9). No species were restricted to the Forested, Patch or Edge locations, but eight species, caught in very low abundance, were unique to the harvested areas (Table 9). Several species were caught in incidental numbers only (<10 individuals).

Treatment comparisons.

The results of single classification ANOVA and TUKEY post-hoc multiple comparisons tests are given in Tables 10 and 11 for the 1996 and 1995 sampling seasons, respectively. Most species were not distinguished by a unique catch in any single treatment type, but were present in varying abundance in many treatments.

Assemblage structure.

Treatment arrangement, as ordinated by the Bray-Curtis index of percent similarity is given in Figure 10. Catches from open areas of clearcuts were consistently isolated from canopy treatments in both years. The 1996 dendrogram obscures this relationship, as the process of central linkage does not precisely reflect original Bray-Curtis similarity

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Table 9. Species of Carabidae occurring in pitfall traps near Smithers, BC. Summary catch data are presented as total number caught throughout the study and the percentage this number comprises of the total catch.

Taxon	Total Caught	% of Catch
**Agonum metallescens* Lec.	3	<0.50
**Amara erratica* Dfts.	2	<0.50
**Amara sinuosa* Casey	13	<0.50
Bembidion fortestriatum Motsch.	7	<0.50
**Bembidion grapei* Gyl.	3	<0.50
Bembidion incertum Motsch.	30	<0.50
**Bembidion incrematum* Lec.	4	<0.50
Bembidion oblongulum Mnh.	169	1.07
Calathus advena Lec.	**3228**	**20.42**
Calathus ingratus Dej.	2	<0.50
Elaphrus americanus Mnh.	1	<0.50
Elaphrus clairvillei Kby.	68	<0.50
**Harpalus laticeps* Lec.	1	<0.50
**Harpalus nigritarsus* Sahlb.	4	<0.50
Leistus ferruginosus Mnh.	5	<0.50
Loricera decempunctata Esch.	14	<0.50
Nebria gyllenhali Schonh.	14	<0.50
Notiophilus sylvaticus Esch.	142	0.90
**Patrobus fossifrons* Esch.	1	<0.50
Pterostichus adstrictus Esch.	259	1.65
Pterostichus castaneus Dej.	290	1.83
Pterostichus empetricola Dej.	29	<0.50
Pterostichus riparius Dej.	125	0.79
Scaphinotus angusticollis Fisch.	**8864**	**56.08**
Scaphinotus marginatus Fisch.	**1008**	**6.38**
Syntomus americanus Dej.	5	<0.50
Trachypachus holmbergi Mnh.	2	<0.50
Trechus chalybeus Dej.	**1506**	**9.53**
Carabidae	**15, 799**	

* Indicates species caught only in harvested areas.

indexes between treatments (Table 12). Relationships were, however, constant from year to year.

Discussion

Catch patterns.

The core/satellite distribution of fauna was proposed by Brown (1984). This hypothesis states that geography is the primary determinant of species distributions, with abundant species being also ones that have extensive geographical ranges. Satellite species will occur with reduced abundance and will be of limited or highly patchy distribution in their entire ranges. Studies from Alberta, Canada, indicate that this pattern existed for ground beetles (Niemelä and Spence 1994).

Here, carabid catches also conformed well to this distribution. The four very abundant species caught all have wide regional distributions (Lindroth 1961, 1966), whereas the others do not (or at least have not been documented in spot collections) or do, but happen to be at the margins of their distributions in the region of the study locale. Some species, like those in the genus *Bembidion* Latreille, occur across wide ranges but only in specific conditions (Lindroth 1963), and thus are present in the landscape (and hence in collections) in relatively small numbers.

In comparison with similar studies, the carabid catch was average to poor in terms of species richness. Craig (1995) lists 28 species from a full year of intensive pitfall

Table 10. Commonly occurring species (n>20) captured in pitfall traps near Smithers, BC, 1996. Comparisons are given for treatment effect on the basis of single-classification ANOVA and TUKEY tests. Treatment codes with a continuous underline were not significantly different from one another (α= 0.05). Treatment codes are: OC=open areas in clearcut; OP=open areas in patch retention; P=patch; E=edge; F=undisturbed forest.

Taxon	Mean ± SE					p-value Treatment Effect
Bembidion oblongulum	0.027± 0.010 OC	0.011± 0.003 P	0.010± 0.006 OP	0.008± 0.002 F	0.001± 0.001 E	**0.011**
Calathus advena	0.851± 0.230 E	0.326± 0.086 P	0.092± 0.020 F	0.092± 0.038 OC	0.010± 0.024 OP	**0.001**
Elaphrus clairvillei	0.024± 0.020 OP	0.004± 0.004 OC	0.001± 0.001 E	0.001± 0.001 P	--- F	0.224
Notiophilus sylvaticus	0.023± 0.009 P	0.011± 0.002 F	0.009± 0.004 OC	0.008± 0.003 E	0.008± 0.003 OP	0.131
Pterostichus adstrictus	0.054± 0.015 OC	0.051± 0.009 OP	0.003± 0.002 E	0.001± 0.001 P	0.001± 0.001 F	**0.001**
Pterostichus castaneus	0.034± 0.012 OC	0.031± 0.011 OP	0.022± 0.005 P	0.013± 0.003 E	0.011± 0.002 F	0.053
Pterostichus riparius	0.014± 0.006 OP	0.013± 0.006 OC	0.004± 0.002 F	0.002± 0.001 P	0.002± 0.001 E	**0.033**
Scaphinotus angusticollis	1.031± 0.134 E	0.743± 0.077 F	0.680± 0.071 P	0.420± 0.067 OP	0.177± 0.034 OC	**0.001**
Scaphinotus marginatus	0.112± 0.061 OC	0.080± 0.019 F	0.066± 0.030 OP	0.050± 0.013 E	0.027± 0.012 P	0.387
Trechus chalybeus	0.319± 0.056 OC	0.153± 0.038 OP	0.064± 0.022 P	0.050± 0.013 E	0.036± 0.006 F	**0.001**

Table 11. Commonly occurring species (n>20) captured in pitfall traps near Smithers, BC, 1995. Comparisons are given for treatment effect on the basis of single-classification ANOVA and TUKEY tests. Treatment codes with a continuous underline were not significantly different from one another (α= 0.05). Treatment codes are: OC=open areas in clearcut; OP=open areas in patch retention; P=patch; E=edge; F=undisturbed forest.

Taxon	Mean ± SE				p-value Treatment Effect
Bembidion oblongulum	0.014 ±0.004 P	0.012 ±0.006 OP	0.008 ±0.003 OC	0.002 ±0.001 F	**0.034**
Calathus advena	0.279 ±0.081 P	0.111 ±0.030 F	0.042 ±0.017 OP	0.008 ±0.005 OC	**0.001**
Elaphrus clairvillei	0.004 ±0.004 OC	0.004 ±0.002 OP	-- P	-- F	0.218
Notiophilus sylvaticus	0.006 ±0.003 F	-- P	-- OC	-- OP	0.179
Pterostichus adstrictus	0.023 ±0.007 OP	0.018 ±0.006 OC	0.001 ±0.001 P	-- F	**0.001**
Pterostichus castaneus	0.015 ±0.005 OP	0.010 ±0.004 OC	0.010 ±0.003 P	0.037 ±0.012 F	0.400
Pterostichus riparius	0.018 ±0.013 P	0.017 ±0.011 OP	0.008 ±0.004 F	0.002 ±0.002 OC	0.476
Scaphinotus angusticollis	0.408 ±0.042 F	0.332 ±0.076 OP	0.329 ±0.411 P	0.118 ±0.026 OC	**0.002**
Scaphinotus marginatus	0.065 ±0.027 OC	0.045 ±0.013 F	0.025± 0.015 P	0.017 ±0.010 OP	0.236
Trechus chalybeus	0.130 ±0.036 OC	0.115 ±0.030 OP	0.082 ±0.040 P	0.019 ±0.005 F	**0.004**

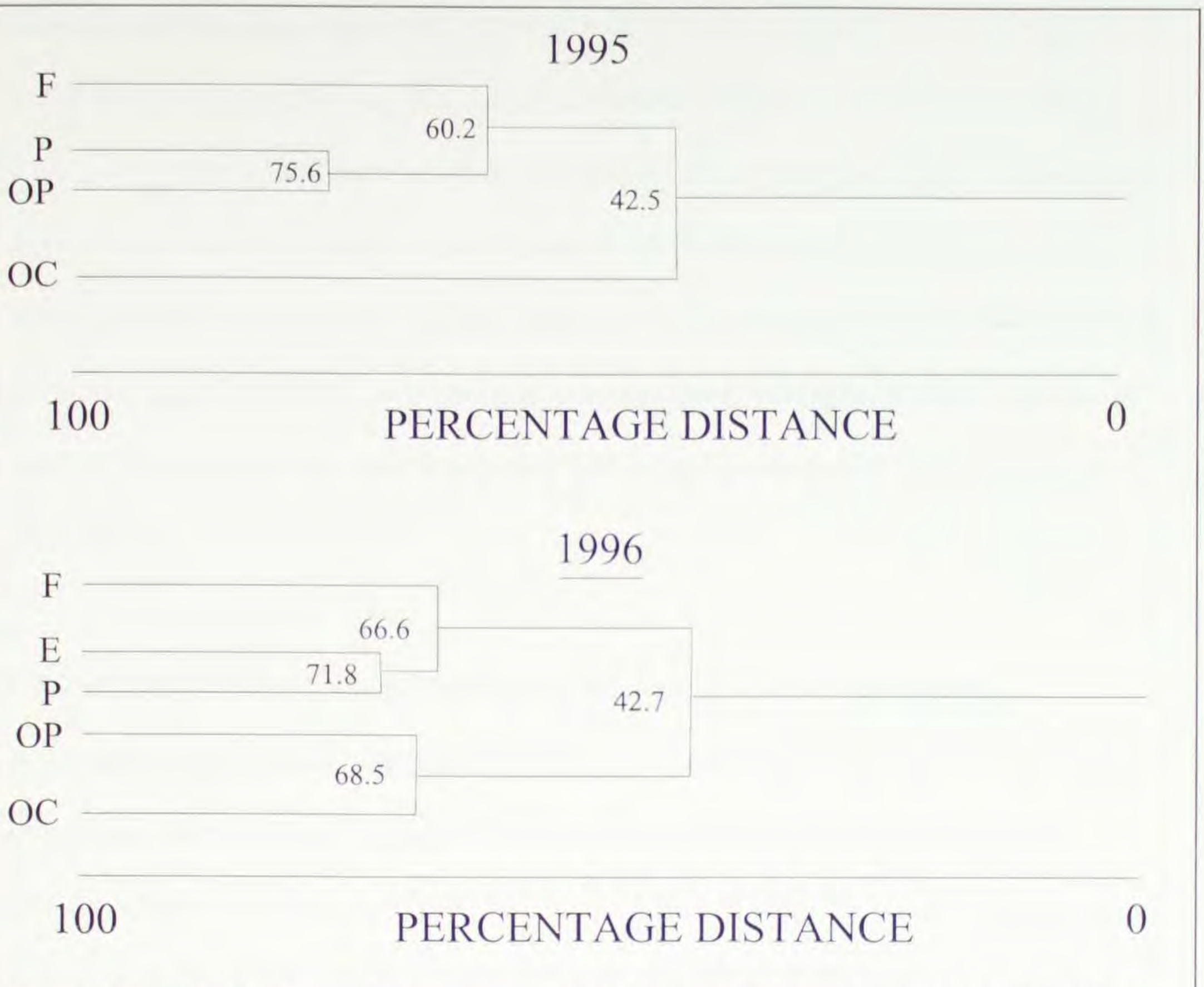

Figure 10. Ordination of treatment types by carabid beetle catch, using cluster analysis of the Bray-Curtis (1957) index of percent similarity. Treatments are denoted by: 'E'=Edge; 'F'=Forest; 'P'=Patch; 'OP'=openings in patch retention harvests; 'OC'= openings in clearcut harvests.

Table 12. Trellis diagram for Bray-Curtis (1957) indexes of similarity, prior to cluster analysis, for Carabidae from pitfall traps near Smithers, BC. Categories refer to harvesting treatments.

Forest	**66**			
Patch	**72**	**67**		
Harvest/ Patch	**42**	**50**	**61**	
Clearcut	**26**	**36**	**40**	**68**
	Edge	**Forest**	**Patch**	**Harvest/ Patch**

trapping on Vancouver Island, BC, Niemelä *et al.* (1993) itemized 39 species from a multi-year study near Hinton, AB, and Duchesne and McAlpine (1992) list 28 species from a single summer of pitfall trapping in eastern Ontario jack pine forest. Assemblages from all three studies, as well as from Spence *et al.* (1996), and Niemelä *et al.* (1992) have been resolved to distinct response categories of: forest generalists (species abundant through a range of local forested habitats), mature-forest specialists (species confined to specific forested habitats) and open-habitat specialists (species occurring primarily in open areas).

Chapter 2 indicated that no species in this study displayed small-scale habitat distributions that could be interpreted as those of a forest specialist. Likewise, none of the species were highly restricted to forested areas, and thus the category of forest generalist does not apply. The emergence of these patterns nullifies the first hypothesis of my study: that species restricted to mature forest would be present also in patches. No species were restricted to mature forest. The fauna in the study area appears to have had a very generalist nature, more so than has been previously described for carabid beetle assemblages.

Instead of these distinct response categories, the majority of the species collected here could be better described with categories representing responses along habitat gradients. For example, the treatments from my study were defined by the degree of harvesting disturbance within which they existed. Conversely, each treatment may be thought to have had a distinct level of "habitat integrity", from which species' abundance may be

determined. This is reminiscent of the index of "old-growth equivalency" used by Coates and Steventon (1995) in which different harvesting systems are compared, given the floristic effects imposed by them. I would propose that an intuitive ordering of treatments for my work, by this means, would be forest>edge>patch>harvested with retention>clearcut harvest. Gradient responses are those in which a species' abundance changes by treatment in a manner representing this ordering. This is logical in that qualities provided by a mature forest would include abiotic and biotic components of a shaded, canopy environment. The total removal of canopy, as in a clearcut, is accompanied by the alteration of many of these features. The partial removal of canopy (e.g. around the edges of cuts, including the boundaries of small patches) will correspondingly retain a partial degree of the original habitat quality, in terms of light, shade, temperature and other factors.

From these results, species can be classified into the following response categories:

1. No response. 2. Forest Gradient. 3. Disturbance Gradient. 4. Disturbance Specialist.

5. Edge/Patch Specialist. This interpretation is presented graphically in Table 13. The gradient trends are consistent from year to year, and may be a reflection of a directional gradient of habitat integrity, which is eroded with increased site disturbance and/or influenced by nearby disturbance. Hence the "gradient" is linear, with two extremes: undisturbed, mature forest and clearcut harvest. The Patch and Edge locations are intermediate between Forest and Open sites, and openings with patch retention maintain more integrity than conventional clearcut harvests, due to associated edge effects (see below).

Table 13. Response classifications of Carabidae collected near Smithers, BC. Categories are based on interpretation of data from Tables 10 & 11, with black representing highest relative population density, and white the least population density.

Category	Treatment				
	Forest	Edge	Patch	Patch Cut	Clearcut
Forest Gradient					
Scaphinotus angusticollis					
Edge/Patch Specialist					
Calathus advena (1995 Patch/1996 Edge)					
Disturbance Gradient					
Trechus chalybeus					
Bembidion oblongulum (**1996**)					
********Pterostichus castaneus* (**1996**)					
Disturbance Specialist					
Pterostichus adstrictus					
********Bembidion oblongulum* (**1995**)					
********Pterostichus riparius* (**1996**)					
No Response					
Elaphrus clairvillei					
Notiophilus sylvaticus					
Pterostichus castaneus (**1995**)					
Pterostichus riparius (**1995**)					
Scaphinotus marginatus					

**A p-value indicating a significant treatment response occurred in these cases. TUKEY tests were unable to differentiate between treatment means, and the categorical interpretation is the author's subjective determination of where differences between means existed.

With a core/satellite catch pattern, species numerous enough for analysis are frequently those with broad geographical distributions, and several species from this study have been collected elsewhere. The published responses of these overlap species to harvest disturbance conflict with my observations, as described above. For example, in my study, *Scaphinotus angusticollis* Fisch. was the dominant species in numbers and size. Craig (1995) also caught this species in high abundance on Vancouver Island, BC, but very rarely in clearcut areas. She thus classified it as a forest generalist, recovering gradually with stand succession. This pattern has apparently been observed near Sicamous, BC, as well (S. Lavallee, [10] pers. comm.). My data indicate that *S. angusticollis* does not respond as a "forest species", that it appears to use harvested areas successfully, and may have some predisposition toward occurring in high densities at stand edges. Lindroth (1961) characterizes it as a true woodland species, inhabiting "vancouverian" forests along the west coast. Despite Dr. C.H. Lindroth's and Dr. G.E. Ball's carabid collections very near the study locale (Lindroth 1961-1969), no collections of this species were made from Smithers, although some were taken near Terrace, BC. It is quite possible that my study site was on the eastern boundary of the species distribution for the latitude.

Likewise, *Scaphinotus marginatus* Fisch., has been demonstrated as a forest generalist (Niemelä *et al.* 1992; Spence *et al.* 1996). My data indicate that this species was a habitat generalist, composed of populations invariant across disturbance types. Craig (1995) collected this species in small numbers only and classified it as unresolved, but her counts indicated that it might also occur as a forest species. Lindroth (1961) indicates the

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species as highly variable in morphology and generally eurytopic. However, it may have regionally variable habitat preferences, being more restricted to forests in southern areas, occurring above timberline in the Rocky Mountains, and throughout open tundra on the Aleutian Islands, AK.

Pterostichus riparius Dej. was the most threatened species from multiple pass rotations of forest harvesting in Alberta lodgepole pine forests, according to Spence *et al.* (1996). This is perhaps the most contrasting example I encountered because my data suggest that this species may prefer open habitat. Like *S. marginatus*, Lindroth (1966) indicates that in the Rocky Mountains, and on Kodiak Island, AK, this species may appear above timberline.

Trechus chalybeus Dej. was more often caught in openings than other treatments (Tables 10 and 11). Spence *et al.* (1996) list this species as a forest specialist, occurring infrequently in openings, and consider it threatened by multiple pass harvest rotations which do not allow the development of mature forest. Lindroth (1961) indicates this species as generally hygrophilous, occurring occasionally above timberline near margins of snow patches.

Calathus advena Lec. has been collected by Spence *et al.* (1996) as a forest specialist threatened by short rotation intervals in Alberta, and by Duchesne and McAlpine (1992) as a species characterizing clearcuts in eastern Ontario. My data, the westernmost collection of the three, indicate that this species is a generalist with high population densities in patch and edge environments. Lindroth (1966) lists this species as primarily a forest insect, in shaded, mesic habitats with sparse vegetation cover. Alternatively, in

the Aleutian Islands, AK, it occurs in open meadows with rich, luxurious vegetation (Lindroth 1966).

Elaphrus clairvillei Kby. was collected as a forest specialist (Niemelä *et al.* 1992), but I collected it abundantly in openings, although the use of ANOVA did not permit discrimination among treatments. *Elaphrus* Fabricius is characterized by Lindroth (1961) as a genus whose members are generally hygrophilous. *E. clairvillei* is more specific in avoiding open spaces, and preferring certain types of soft soil, interspersed with specific vegetation.

Finally, *Pterostichus adstrictus* Esch. was the only common species between this and other studies with agreed response patterns to harvesting disturbances, confirming it as an overall generalist (Niemelä *et al.* 1993; Spence *et al.* 1996). Also, this is the only species throughout these collections for which there is substantial documentation of life history (Goulet 1974). It was characterized in that study as preferring open habitat, needing moist wood to lay its eggs in. This is in agreement with Lindroth (1966).

The harvests I measured ranged in age from 4-6 years, and it is possible that populations therein may still be in a state of "scatter" from harvest disturbance, having not completely abandoned those sites. *Pterostichus riparius* and *Calathus advena* are especially suspect as Spence *et al.* (1996) have observed these species to occur more frequently in clearcuts than in mature forests at two years post-harvest, but to be almost absent from stands by 9 years post-harvest. Exactly when this decline occurs is unclear, and it is likely regionally

variable. *Scaphinotus marginatus* was demonstrated to disappear immediately from sites at ages of 2 years post-harvest (Niemelä *et al.* 1993; Spence *et al.* 1996), and 3-8 years (Craig 1995). *Scaphinotus angusticollis* has been demonstrated to be immediately eliminated from harvests of 3-8 years' age (Craig 1995), and young stands of the ESSF subzone near Smithers, BC (G.G.E. Scudder[11], pers. comm.). The consistency of my results from year to year, given the young age of the stands, indicates some stability in population structure, which would be contrary to temporally declining density. However, if there is a threshold at which some species are eliminated from clearcut harvests, then my classifications would be subject to revision.

Assuming however that they are correct, I propose three possible explanations for these discrepancies: disturbance-oriented, geographic variation-oriented, and species-oriented.

Disturbance-oriented. The colonization of potential habitats is dependent upon source populations, capable of dispersing to, and reproducing in, new localities. When considering the establishment of pre-harvest carabid assemblages, it has been recognized that there must remain substantial numbers in surrounding contiguous forest to do so (Ås 1993; Howe *et al.* 1991). The same is true for openings. Typically, regeneration or meadow specialists of Carabidae are dominated by members of the genera *Amara* Bonelli and *Harpalus* Latreille (Craig 1995; Duchesne and McAlpine 1992; Niemelä *et al.* 1993, 1992; Spence *et al.* 1996). These genera were virtually absent from my entire collection, but are common in other studies.

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Lindroth (1968) states members of *Amara* Bonelli as being xerophilous, occurring primarily in open country with large, weedy vegetation of sparse density. Adults are presumed to be primarily herbivores (Lindroth 1968), although there are few data to support this. *Harpalus* Latrielle adults apparently have similar preferences of habitat and food, and often occur together with populations of *Amara*. Clearcut areas for my study fit these habitat descriptions accurately, with large quantities of fireweed (*Epilobium angustifolium*) reaching heights of 2+ m. The sites were not, however, decidedly xeric, but highly variable with respect to moisture, changing across the season and with prevalent precipitation patterns. Lindroth (1968) documents several species from both genera that could abundantly populate this region. This missing fauna may partially account for the moderate species richness observed in this site.

One hypothesis for this absence is the degree of disturbance in the landscape. The Copper River Valley, at the time of sampling, had very little harvesting, although fire has been an important part of the Engelmann Spruce-Subalpine Fir Biogeoclimatic Subzone (Parminter 1983). The particular biogeoclimatic subzone this work was carried out in (ESSFwv; Meidinger and Pojar 1991) is thought to have had the least amount of natural disturbance of all subzones of the ESSF (BC M.O.E/M.O.F 1995). There is evidence that certain insect species which are specialists of newly created forest openings, including some Carabidae, are particularly attracted to clearings created by fire (Evans 1971; Harris and Whitcomb 1974; Holliday 1984, 1991). Although a comparison between harvesting and fire for insect colonization has been

only cursorily investigated (Wikars 1995), differential attraction and habitat quality between the two is a distinct possibility (Myers 1990; Wikars 1995).

Colonization of clearcuts by capable specialist species could then be hampered by lack of source populations present in the landscape and/or lack of attractive qualities of harvested areas, resulting in reduced competition in the newly created openings. The absence of *Amara* and *Harpalus* species may underlie a more general absence of a wide array of species from other taxa that could otherwise compete with the "forest" fauna for establishment.

Geographic-location-oriented. The western longitude of the study site predisposes it to wetter and cooler regimes before and after harvesting, which may deter these xerophilous (Lindroth 1968) genera. The altitude of the site (1000 m), with its short growing season, may select for specific species with cold-adapted overwintering strategies and alpine-oriented life histories (e.g. Sota 1986). Members of the genus *Scaphinotus* Dejean have been trophically characterized as a gastropod predators (Lindroth 1961), following mucous trails of their prey (Digweed 1993), which were quite abundant in my pitfall catches. One possible reason for differential regional habitat responses may be predator-prey tracking. Gastropod occurrence in traps east of the Rocky Mountains is typically quite reduced when compared with the abundance I observed (J. Spence[12], pers. comm.), and these prey populations could be more severely limited by differential clearcut conditions between there and here.

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One of the central themes in Lindroth's (1961, 1966) ecological descriptions is the tendency for forest species to emerge into open habitat in certain limits of their distributions, often western. This may underlie a simple moisture requirement, which is met in coastally-influenced western areas, but in southern or eastern ranges is denied in open areas. John Spence[13] (pers. comm.) described the pine stands of his Alberta studies as becoming quite xeric after harvesting. This is contrasted to the Bulkley Valley/Terrace region where conditions will remain very wet in harvests, with high abundance of lush vegetation (see previous reference to fireweed at this site).

Species-oriented. The genus *Scaphinotus*, especially *S. marginatus*, is prone to subspeciation, difficult to observe in external morphology (Lindroth 1961). Such changes are prerequisite to speciation, a process in carabids requiring the geographic isolation of species (Kavanaugh 1976). We may expect that species with large contiguous ranges may have fragmented populations at their distribution limits, capable of varying morphologically and ecologically (George Ball[14], pers. comm.). Three of the study species reach their distributional limits in the study area: *S. angusticollis*, *S. marginatus*, and *P. riparius* (Lindroth 1961, 1966).

Treatment comparisons.

"Integrity" of habitat may include many factors, defined for the specific requirements of each species. For example, reduction of canopy closure from dieback in maple hardwood

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forests has been negatively correlated with carabid species richness (Martel *et al.* 1991), which the authors conjecture to be the effects of microclimatic change. Other factors, like structural characters, e.g. dead wood, have been demonstrated to be critical in maintaining rare species of Coleoptera (Siitonen and Martikainen 1994). When harvesting occurs, the forest canopy is removed, machinery and timber are moved over the litter surface, and many important microclimatic factors are changed. The "integrity" of the original habitat, with respect to the original biota, becomes eroded. Currently, structural features of canopy are the only measures of "old-growth equivalency" among harvesting systems that incorporate the retention of live trees within harvested areas.

Effects may extend beyond the boundaries of the harvested area. Microclimatic changes at stand edges have been demonstrated to change in the contexts of increased light, altered air movements, litter moisture, and temperature regimes (Carmago and Kapos 1995; Chen *et al.* 1993; Matlack 1993; Palik and Murphy 1990). Atmospheric deposition of simple nutrient compounds can be concentrated at stand edges (Beier and Gunderson 1989). Microclimatic effects are usually interpreted as ecotones, decreasing gradually with distance from stand edge.

Edges are known to have altered plant communities (de Casenava *et al.* 1995; Matlack 1994), and have been demonstrated to influence animal (Stamps *et al.* 1987). Edges have permanent, long-range effects on forest stands by interacting with, and altering vegetation dynamics of the forest interior (Ranney *et al.* 1981). Laurance (1991) indicates that in Queensland, Australia, circular forest reserves must exceed 2000-4000 ha in order that

50% of the reserve remains unaffected by microclimatic changes influenced from edge boundaries.

Some species of carabid beetles are thought to be influenced by stand edges in stand-level distributions. Spence *et al.* (1996) have shown that at 80 m from the stand edge, species that were previously thought to be specialists of either open or forested habitat could be trapped in the opposing treatment type. Thus we might expect that the geometry of forest edges, at the stand and at the landscape level, might influence the distributions of either type of specialist. This underlies a primary difference between clearcut and patch retention harvesting. The volume of cut is not necessarily reduced, only rearranged to allow the placement of patches. With a constant harvest area, patches are produced at the expense of increasing the edge boundary of the harvest.

My second hypothesis, that patches will harbour assemblages equivalent to those occurring in mature forest, is partially validated. According to the Bray-Curtis analysis and to the distribution patterns of some species, assemblages in patches are equivalent to those occurring at stand edges, and intermediate between those of openings and those of undisturbed forest. This is further validation of the "integrity" concept.

Edge effects from stand edges and from patches can thus be seen to influence the composition of faunas in openings (Duelli 1990). I would propose this to explain the differences between openings in clearcuts and openings in patch retention harvests. Catches from patch openings were distinct from clearcuts with respect to a single species only: *Trechus chalybeus* Dej. (1996 data). However, the order in which mean catches

rank, according to their quantities, is consistent from year to year for several species. The cumulative effect of this is reflected in the differentiation of the clearcut from all other treatments in cluster analysis.

It is possible that increased sampling would yield significant differences between opening types for several species. The third hypothesis, that patch retention openings would have a carabid fauna more similar to forests than clearcuts, appears to be true.

Implications for patch retention.

The decision to use patch retention over clearcut harvesting, while removing a standard area of timber from the landscape, will change the geometry of fragmentation. In the initial stages of harvesting, there is a noticeable difference in fauna between opening types of the two systems. The difference does not seem large enough to prevent clearcuts from recovering a pre-harvest fauna.

However, this particular landscape, like many others in BC, will see dramatic increases in harvesting-related disturbance. If my conjecture regarding an associated increase in the colonization of open-habitat specialists is correct, the forest fauna will correspondingly encounter increased competition in post-harvest openings. Spence *et al.* (1996) hypothesize that the failure of forest specialists like *Scaphinotus marginatus* Fisch. to recolonize available habitat even 27 years post-harvest, was due to dwindled source populations in the landscape. This insufficiency was thought to result from habitat loss and the insularization of remaining stands.

Patch size in my harvesting treatments ranged from 0.1-2.0 ha. According to Halme and Niemelä (1993), this fragment size range can be highly influenced by open-habitat specialists, maintaining forest generalists, but losing forest specialists. The perpetual maintenance of forest species requires fragments of much larger size. Thus, patches in patch retention harvesting may be exchanging individuals with the surrounding mature forest, and helping to maintain forest species in openings, but under a larger degree of landscape alteration, cannot be expected to maintain this function.

The use of harvesting strategies, like patch retention, have important conservation value for invertebrates, but this value is contextual. It is dependent on the surrounding forest matrix to provide conditions in which there are abundant source populations of forest colonizers and a not too abundant source of open-habitat specialists, which can penetrate well into forest interiors (Spence *et al.* 1996).

The commitment to conservation of biota in an operational landscape must extend beyond the alteration of spatial disturbance patterns. The increased costs of patch retention harvesting are likely justified only if accompanied by an effort to maintain high levels of contiguous forest in the landscape. This is concurrent with the notion that strategies like patch retention can be used to mimic structural retention at the stand level. They can, and will be effective. But structural retention at the landscape scale must be pursued concurrently in order to mimic natural disturbance patterns of biological organization. This can be accomplished by emulating pre-harvest frequencies of openings: both spatial and temporal patterns must be considered.

Specific Study Conclusions

Carabid beetle assemblages from undisturbed forest are similar to those found in both edge and patch habitats. However, hypothesis number one (that patches would support populations of mature forest specialists) is precluded as there were no demonstrated mature forest specialists or generalists. Hypothesis two (that patches would support assemblage patterns of carabid species similar to mature forest) was validated.

The response of assemblages to the patch treatment was encouraging in terms of being an effective means to promote the regeneration of pre-harvest carabid assemblages. Hypothesis three (that patch retention openings would support carabid assemblages more similar in nature to mature forest than those occurring in conventional clearcuts) was validated.

Differences between this study and similar ones in western Canada can possibly be attributed to differences in elevation, latitude and longitude, and degree of forest fragmentation in the landscape. Assemblage-level response of carabid beetles to tree harvests may be regionally variable.

Given point three, patch retention may be increasingly important as a regenerative tool, when there is increased disturbance in the landscape. However, there is possibly a disturbance threshold at which patches will no longer receive populations from surrounding contiguous forest, or would experience significant influx from disturbance

specialists, and would become inert with respect to the conservation and regeneration of forest-dwelling carabid assemblages.

Bibliography

Ås, S. 1993. Are habitat islands islands? Woodliving beetles (Coleoptera) in deciduous forest fragments in boreal forest. *Ecography* 16: 219-28.

Barbour, M. G., J. H. Burk, and W. D. Pitts. 1987. *Terrestrial Plant Ecology*. Don Mills, Ont.: Benjamin Cummings.

BC Min. Env./Min. For. 1995. *Biodiverstiy Guidebook.* Forest Practices Code Guidebooks. Province of BC, Victoria, BC.

BC Min. For./Min. Env. 1995. *Silvicultural Systems Guidebook.* Forest Practices Code Guidebooks. Province of BC, Victoria, BC.

Beier, C., and P. Gundersen. 1989. Atmospheric deposition to the edge of a spruce forest in Denmark. *Environ. Pollut.* 60: 257-71.

Bray, J. R., and C. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27: 325-49.

Brown, J. H. 1984. On the relationship betwen abundance and the distribution of species. *Am. Nat.* 124: 255-79.

Carmago, J. L. C., and V. Kapos. 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. *J. Trop. Ecol.* 11: 205-21.

Chen, J., J. F. Franklin, and T. A. Spies. 1993. Contrasting microclimates of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology*: 219-37.

Coates, D. K., and D. J. Steventon. 1995. Patch retention harvesting as a technique for maintaining stand level biodiversity in forests of north central British Columbia. pp. 102-6 *in*: Bamsey, C. R., ed. *Innovative Silvicultural Systems in Boreal Forests.* Conference Proceedings, October 2-8, 1994, Edmonton, AB. Clear Lake Ltd., Edmonton, AB.

Coupé, R., A. C. Stewart, and B. M. Wikeem. 1991. Chapter 15: Engelmann Spruce-Subalpine Fir Zone. pp. 223-36 *in*: Meidinger, D., and J. Pojar, eds. *Ecosystems of British Columbia.* Special Report Series, Number 6. Victoria, BC: BC Ministry of Forests.

Craig, K. G. 1995. Variation in Carabid Community Structure Associated with Coastal Douglas-fir Forest Successional Stages. M.Sc. Thesis, University of British Columbia, Dept. Zool. Vancouver, British Columbia.

de Casenava, J. L., J. P. Pelotto, and J. Proromastro. 1995. Edge-interior differences in vegetation structure and composition in a Chaco semi-arid forest, Argentina. *For. Ecol. & Mgt.* 72: 61-69.

de Vries, H. 1996. Metapopulation structure of *Pterostichus lepidus* and *Olisthopus rotundatus* on heathland in the Netherlands: the results from transplant experiments. *Ann. Zool. Fenn.* 33: 77-84.

de Vries, H. H., and P. J. Den Boer. 1990. Survival of populations of *Agonum ericeti* Panz. (Col., Carabidae) in relation to fragmentation of habitats. *Neth. J. Zool.* 40 (3): 484-98.

DeLong, S. C., and D. Tanner. 1996. Managing the pattern of forest harvest: lessons from wildfire. *Biodiversity & Conserv.* 5: 1191-205.

den Boer, P. J. 1977. *Dispersal power and survival. Carabids in a cultivated countryside.* Miscellaneous Papers 14. Landbouwhogeschool Wageningen, The Netherlands.

den Boer, P. J. 1986. Carabids as objects of study. pp. 539-51 *in*: den Boer, P. J., M. L. Luff, D. Mossakowski, and F. Weber, eds. *Carabid Beetles - Their Adaptations and Dynamics.* Stuttgart, Germany: Gustav Fischer.

Digweed, S. C. 1993. Selection of terretrial gastropod prey by cychrine and pterostichine ground beetles (Coleoptera: Carabidae). *Can. Ent.* 125: 463-72.

Duchesne, L. C., and R. S. McAlpine. 1992. *Using carabid beetles as a means to investigate the effect of forestry practices on soil diversity.* PNFI Technical Report 16. Forestry Canada, Petawawa National Forestry Institute.

Duelli, P. 1990. Population movements of arthropods between natural and cultivated areas. *Biol. Conserv.* 54: 193-207.

Eberhardt, K. E., and P. M. Woodward. 1987. Distribution of residual vegetation associated with large fires in Alberta. *Can. J. For. Res.* 17: 1207-12.

Evans, W. G. 1971. The attraction of insects to forest fires. pp. 115-27 *in*: *Tall Timbers Conference on Ecology of Animal Control by Habitat Management.* Conference Proceedings, 1971.

Eyre, M. D., M. L. Luff, S. P. Rushton, and C. J. Topping. 1989. Ground beetles and weevils (Carabidae and Curculionidae) as indicators of grassland management practices. *J. Appl. Ent.* 107: 508-17.

Farnden, C. 1994. *Forest regeneration in the ESSF zone of north-central British Columbia.* Information Report BC-X-351. Canadian Forest Service, Pacific and Yukon Region, Pacific Forestry Centre, Victoria, BC.

Forbes, Inc. 1996. *American Heritage Dictionary of the English Language*. Houghton Mifflin.

Franklin, J. F., D. A. Perry, T. D. Schowalter, M. E. Harmon, A. McKee, and T. A. Spies. 1989. Importance of ecological diversity in maintaining long-term site productivity. pp. 82-97 *in*: Perry, D. A., R. Meurisse, B. Thomas, R. Miller, J. Boyle, J. Means, C. R. Perry, and R. F. Powers, eds. *Maintaining Long-Term Productivity of Pacific Northwest Forest Ecosystems.* Portland, OR.: Timber Press.

Goulet, H. 1974. Biology and relationships of *Pterostichus adstrictus* Eschsholtz and *Pterostichus pennsylvanicus* LeConte (Coleoptera: Carabidae). *Quaestiones Entomologicae* 10: 3-33.

Hall, D. W. 1991. The environmental hazard of ethylene glycol in insect pit-fall traps. *Coleopt. Bull.* 45 (2): 193-94.

Halme, E., and J. Niemelä. 1993. Carabid beetles in fragments of coniferous forest. *Ann. Zool. Fenn.* 30: 17-30.

Hammond, H. 1991. *Seeing the Forest Through the Trees*. Vancouver, BC: Polestar .

Harris, D. L., and W. H. Whitcomb. 1974. Effects of fire on populations of certain species of ground beetles (Coleoptera: Carabidae). *Fla. Ent.* 57: 97-103.

Harrison, S. 1993. Metapopulations and Conservation. pp. 111-28 *in*: Edwards, P. J., R. M. May, and N. R. Webb, eds. *Large-Scale Ecology and Conservation Biology.* Cambridge, MA: Blackwell Science.

Heijerman, T., and H. Turin. 1994. Towards a method for biological assessment of habitat quality using carabid samples (Coleoptera, Carabidae). pp. 305-12 *in*: Desender, K., M. Dufrêne, M. Loreau, M. L. Luff, and J.-P. Maelfait, eds. *Carabid Beetles: Ecology and Evolution.* Netherlands: Kluwer Academic Publishers.

Holliday, N. J. 1984. Carabid beetles (Coleoptera: Carabidae) from a burned spruce forest (Picea spp.). *Can. Ent.* 116: 919-22.

Holliday, N. J. 1991. Species responses of carabid beetles (Coleoptera: Carabidae) during post-fire regeneration of boreal forest. *Can. Ent.* 123: 1369-89.

Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of 'sink' populations. *Biol. Conserv.* 57: 239-55.

Kavanaugh, D. 1976. Rates of taxonomically significant differentiation in relation to geographical isolation and habitat: examples from a study of the nearctic *Nebria* fauna. *in*: Erwin, T. L., G. Ball, and D. R. Whitehead, eds. *Carabid Beetles: Their Evolution, Natural History and Classification.* Boston: The Hague.

Laurance, W. F. 1991. Edge effects in tropical forest fragments: application of a model for the design of nature reserves. *Biol. Conserv.* 57: 205-19.

Lindroth, Carl. H. 1961-1969. *The Ground-Beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska.* (Suppl.) 20 (1961), 24 (1963), 29 (1966), 33 (1968), 34 (1969), & 35 (1969). Lund University, Sweden: Opuscula Entomologica.

Mackenzie, K., and D. Steventon. 1996. *Bird use of a patch retention treatment in SBSmc forests.* Forest Sciences Extension Note # 16. BC Ministry of Forests, Smithers, BC.

Mackinnon, A., J. Pojar, and R. Coupé, eds. 1992. *Plants of Northern British Columbia.* Edmonton, Alta: Lone Pine Publishers.

Maelfait, J.-P., and K. Desender. 1990. Possibilities of short-term carabid sampling for site assessment studies. *in*: Stork, N. E., ed. *The Role of Ground Beetles in Ecological and Environmental Studies.* Andover, UK: Intercept.

Martel, J., Y. Maufette, and S. Tousignant. 1991. Secondary effects of canopy dieback: the epigeal carabid fauna in Québec appalachian maple forests. *Can. Ent.* 123: 851-59.

Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biol. Conserv.* 66: 185-94.

Matlack, G. R. 1994. Vegetation dynamics of the forest edge-trends in space and successional time. *J. Ecol.* 82: 113-23.

Meidinger, D., and J. Pojar. 1991. *Ecosystems of British Columbia.* Special Report Series Number 6. BC Ministry of Forests, Victoria, BC.

Mossakowski, D., H. Främbs, and A. Baro. 1990. Carabid beetles as indicators of habitat destruction caused by military tanks. pp. 237-43 *in*: Stork, N. E., ed. *The Role of Ground Beetles in Ecological and Environmental Studies.* Andover, Hampshire: Intercept Ltd.

Myers, R. L. 1990. Scrub and high pine. pp. 150-193 *in*: Myers, R. L., and J. J. Ewel, eds. *Ecosystems of Florida.* Orlando, FL: University of Central Florida Press.

Niemelä, J. K., and J. R. Spence. 1994. Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. *Ecography* 17: 166-75.

Niemelä, J., D. Langor, and J. R. Spence. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in Western Canada. *Conserv. Biol.* 7 (3): 551-61.

Niemelä, J., J. R. Spence, and D. H. Spence. 1992. Habitat associations and seasonal activity of ground-beetles (Coleoptera, Carabidae) in central Alberta. *Can. Ent.* 124: 521-40.

Noss, R. F., and A. Y. Cooperrider. 1994. *Saving Nature's Legacy - Protecting and Restoring Biodiversity*. Washington DC, USA: Island Press.

Palik, B. J., and P. G. Murphy. 1990. Disturbance versus edge effects in sugar-maple/beech forest fragments. *For. Ecol. Man.* 32: 187-202.

Parminter, J. 1983. Fire history and fire ecology in the Prince Rupert Forest Region. pp. 1-36 *in*: Trowbridge, R. L., and A. Macadam., eds. *Prescribed fire: forest soil symposium*. BC Ministry of Forests, Land Management Rep. 16, Victoria, BC.

Pearson, D. L., and F. Cassola. 1992. World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. *Conserv. Biol.* 6 (3): 376-91.

Pickett, S. T. A., and P. S. White. 1985. *The Ecology of Natural Disturbance and Patch Dynamics* . Toronto: Academic Press, Inc.

Pielou, C. 1984. *The Interpretation of Ecological Data*. Toronto: John Wiley & Sons.

Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. pp. 67-95 *in*: Burgess, R. L., and D. M. Sharpe, eds. *Forest Island Dynamics in Man-dominated Landscapes*. New York: Springer-Verlag.

Refseth, D. 1980. Ecological analyses of carabid communities - potential use in biological classification for nature conservation. *Biol. Conserv.* 17: 131-41.

Schowalter, T. D., R. N. Coulson, and D. A. Crossley, Jr. 1981. Role of southern pine beetle and fire in maintenance of structure and function of the southeastern coniferous forest. *Environ. Ent.* 15 (6): 821-25.

Schowalter, T. D., W. W. Hargrove, and D. A. Jr. Crossley. 1986. Herbivory in forested ecosystems. *Annu. Rev. Entomol.* 31: 177-96.

Shuggart, H. H. 1984. *A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models*. NY: Springer-Verlag.

Siitonen, J., and P. Martikainen. 1994. Occurence of rare and threatened insects living on decaying *Populus tremula*: A comparison between Finnish and Russian karelia. *Scand. J. For. Res.* 9: 185-91.

Sota, T. 1986. Carabid populations along an altitudinal gradient: life history variation of *Leptocarabus kumagaii* (Coleoptera: Carabidae). pp. 139- 147 *in*: den Boer, P. J., M. L. Luff, D. Mossakowski, and F. Weber, *Carabid Beetles: Their adaptations and dynamics*. New York: Gustav Fischer.

Southwood, T. R. E., V. K. Brown, and P. M. Reader. 1979. The relationships of plant and insect diversities in succession. *Biological Journal of the Linnean Society* 12: 327-48.

Spence, J. R., D. W. Langor, J. K. Niemelä, H. A. Càrcamo, and C. R. Currie. 1996. Northern forestry and carabids: the case for concern about old-growth species. *Ann. Zool. Fenn.* 33: 173-84.

Spence, J. R., and J. K. Niemelä. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. *Can. Ent.* 126 : 881-94.

Stamps, J. A., M. Buechner, and V. V. Krishnan. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. *Am. Nat.* 129 (4): 533-52.

Stork, N. E. 1987. Guild structure of arthropods from Bornean rain forest trees. *Ecol. Ent.* 12: 69-80.

Stork, N. E. 1991. The comparison of the arthropod fauna of Bornean lowland rainforest trees. *J. Trop. Ecol.* 7: 161-80.

Systat Corporation. 1997. *Systat 7 for Windows*. Chicago: SPSS Inc.

Thiele, H. U. 1977. *Carabid Beetles in their Environments*. Berlin: Springer-Verlag.

Wikars, L. 1995. Clear-cutting before burning prevents establishment of the fire-adapted *Agonum quadripunctatum* (Coleoptera: Carabidae). *Ann. Zool. Fenn.* 32: 375-84.

Winchester, N. N., and R. A. Ring. 1996. Centinelan extinctions: extirpation of northern temperate old-growth rainforest arthropod communities. *Selbyana* 17 (1): 50-57.

Zar, J. H. 1984. *Biostatistical Analysis*. Englewood Cliffs, N.J. USA: Prentice-Hall, Inc.

Concluding remarks: Difficulties with scale and purpose.

The struggle for the conservation of biological diversity is a complex of basic questions including "what?", "why?" and "how?" (Bunnell 1991; Wilson 1986). I have proceeded to this point with some very focused aspects of "how?" This in itself is a daunting issue, assuming that the pre-requisite questions have been dealt with, which they have not. I will come back to that issue, but would first like to examine how the results of my thesis work will be applicable to conservation in a larger sense, outside the boundaries of the locality in which it occurred. Chapters one and two have focused on small-scale distribution of carabid beetles (either across ecosystem types, or in the occurrence of trap types). The sense of those chapters has been to support the common view of carabids as ecological generalists (Lovei and Sunderland 1996), showing limited small-scale specificity toward habitat features. Chapter 3 further corroborated the generalist notion by showing an uncharacteristic lack of response from carabids to forest harvesting treatments. The differences, however, between the two harvesting treatments, indicates that the matrix of surrounding forest, at the stand level, can make a difference in the activity density of carabid beetles, from 4-6 years post-harvest. In other words, despite the generalist nature of carabid beetles, the structure of the matrix within which a disturbance occurs may have demonstrable short-term consequences for carabid populations.

Establishing the importance of the matrix structure with any certainty is problematic due to a lack of supporting scientific literature with which interpolations to larger scales can

be made. Large-scale or holistic perspectives are important, but frequently ignored in the interpretation of biological data of a localized origin (May 1993). My study is a classic example of this in that its financial funding intended to produce a tangible product for designing the conservation of litter fauna. However, it is impossible to make recommendations over the spatial and temporal scales for which management is needed, even if just for British Columbia. In fact it is difficult even to say how the results of the study may be applied to the immediate landscape in which it occurred.

Biological processes at differing scales do not occur in isolation but in the context of what is happening around and within them. We would wish then to be able to consider scale when managing natural resources. The bottleneck of extrapolation is in part due to limitations in current understanding of the interaction of processes occurring at different spatial and temporal scales. It is also due in part to our lack of understanding of how regional variation can differentially influence the responses of widespread species, and of species assemblages.

British Columbia as an example.

In British Columbia forestry dictates a conspicuous degree of land use. This industry accounts for at least twenty percent of the Province's gross domestic product (BC For. Res. Comm. 1991) and is deeply entrenched in the identity of BC. In resource-dependent communities like Williams Lake and Castlegar forestry-related employment may be as high as 67% (BC For. Res. Comm. 1991). For many years the forest resources of the Province have been taken for granted in providing an immense wealth and infrastructure;

this is changing with forests being increasingly at the heart of social conflict. The BC Forest Practices Code (hereafter referred to as "The Code") was introduced in 1993-94 (Prov. BC 1993), perhaps in response to the changing values our society is placing on forests and nature and the admittedly poor job of Industry and Government in regulating responsible stewardship.[15] The code is a legally enforceable document under which forest harvesting practices are provincially and regionally standardized. With respect to forest harvesting, it is The Code that addresses most pertinently the maintenance of ecologically sound practice in the utilization matrix.

The Code has a "Vision" of "Sustainable use of forests we hold in trust for future generations". Sustainability is defined with the following concepts: encompassing need for present and future generations; a provision of stewardship based on respect for the land; balancing multifaceted needs of the land including productive, spiritual, recreational, economic and cultural (including First Nations); conservation of biological and scenic diversity; and restoration of damaged ecologies (Prov. BC 1994).

The Code and its vision are represented at an operational level with a series of guidebooks for selected topics and practices. Biological diversity is addressed in the "Biodiversity Guidebook" (BC Min. For./Min. Env. 1995), which puts forth that: "The intent is to maintain in perpetuity all native species across their historic ranges." This statement, despite its limitations in implying only species as a level of organization in

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[15]The commonly seen logo on early Forest Practices Code publications includes the caption "Changing the way we manage our forests. Tough Enforcement".

biological diversity to be conserved, delimits the broad objective: namely that all the pieces are important.

The fallout of these policy movements can be seen in the Copper River Valley, where my study was performed. In a functional sense the Copper River Valley is an important drainage to the Bulkley system. It provides many tangible resources to humans including timber, recreation, spawning grounds for salmonid fish, and clean water. It also harbours an impressive biota and complex ecosystems. It is unique in that it has ecosystem classifications of ESSF and Sub-boreal Spruce, similar to surrounding landscape units within the Timber Supply area (Fig. 11), but also contains some coastal influence from Coastal Western Hemlock occurring in its western boundaries.

The design for future harvesting consists of landscape approaches with core areas and corridor areas connecting them (Fig. 11): practices that are popular in conservation texts (Primack 1993; Noss and Cooperrider 1994). Efforts like patch retention are being implemented in the matrix surrounding the protected areas, and an effort to representatively include all BEC zones, subzones and variants has been made (Bulkley Forest District 1997). And despite the large area over which my study was conducted, I will be unable to even conjecture on the appropriateness of the landscape design. Again, this is a problem of scale. The province has appropriately taken the leap to manage forests in a systems-oriented fashion, with a large spatial and time reference. But commitment to biological research must follow the same paths. And union across

different regions toward similar methods in the measurement of biological diversity must be made to further support such an effort.

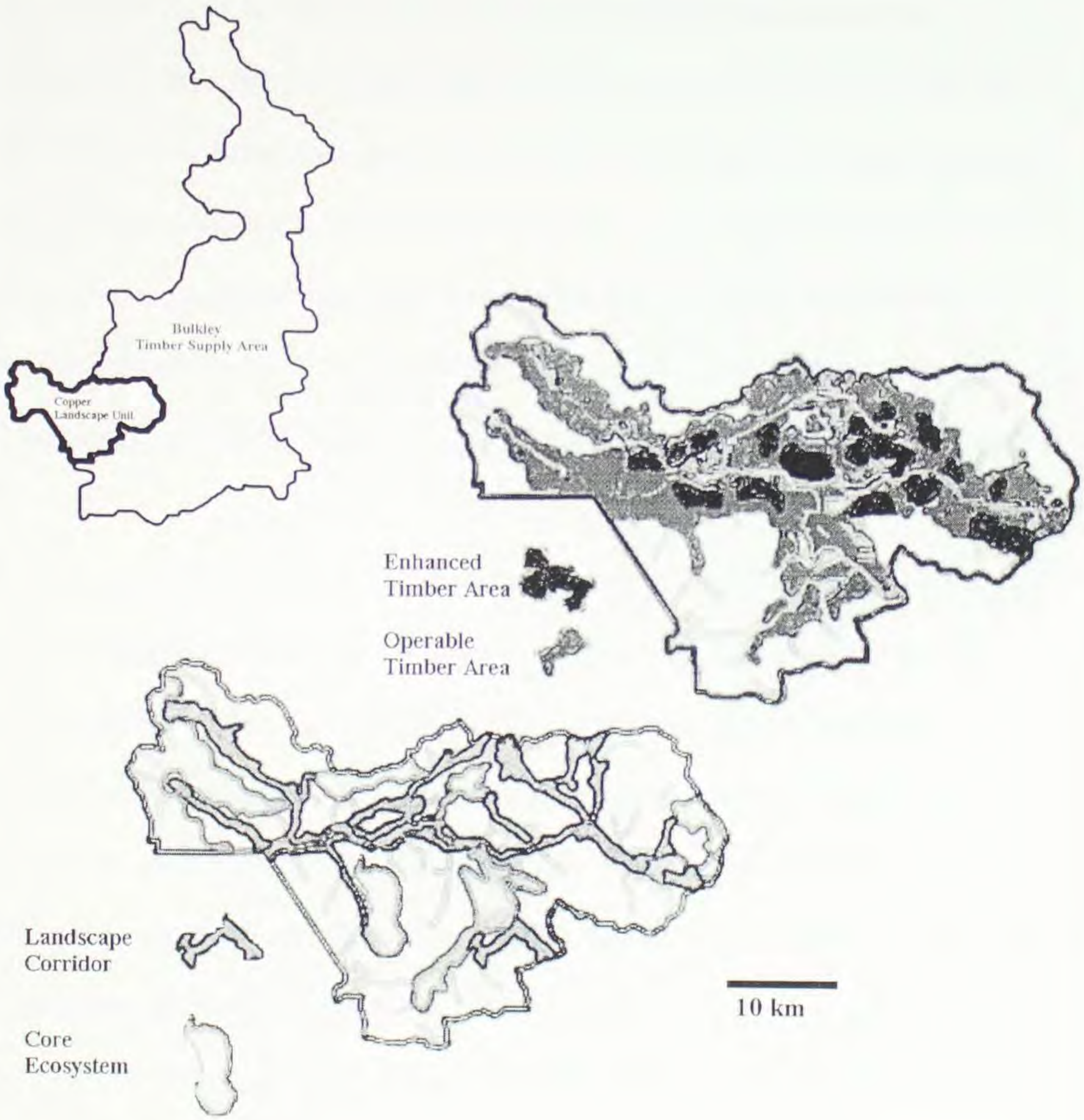

Figure 11. Bulkley Valley Timber Supply Area, British Columbia. The Copper River Landscape Unit is exploded twice, showing both harvested and protected designations.

Scale.

In an ecological sense, scale has been defined as the temporal and spatial characteristics of energy and matter within and among ecological systems (Hoekstra *et al.* 1991). Hierarchy theory (Pattee 1973) was the first structured treatment of scalar ideas in ecology, and continues to influence concepts in describing the organization and distribution of ecosystems (Meidinger and Pojar 1991) and communities (Niemelä and Spence 1994). It describes a direct correlation between scale quantity, and the strength of factors arising at that scale, in determining the distribution of organisms at smaller scales. So processes perceivable at large temporal or spatial scales strongly influence the possibilities of the species organizations which can occur at smaller scales. It is a top-down approach and does not stress any concept of feedback from smaller to larger scales.

Hoekstra *et al.* (1991) have stressed that scale has been an important determinant in the types of organisms that have been chosen to study certain ecological processes. For example, plants have been the primary focus for the study of ideas in biological communities, whereas animals have been largely sought to understand population dynamics, e.g., in island biogeography theory. The choices are ones of convenience, based on scalar implications. Plants are sessile and therefore easy to observe. The scale over which one must travel to gather data is reasonable. For most terrestrial animals, vagility is an important quality, making them energy-intensive to study. For the same reasons, population dynamics and island biogeography have been studied mostly for animals, which colonize and fluctuate in a temporal scale for which data collection is convenient. Similarly, current large-scale spatial distribution of assemblages has been

sought primarily for tree species, which can be accurately interpreted from remote sensing techniques at continental and global scales. Thus our understanding of scalar processes is biased toward convenient taxa. Our understanding of scale-based processes is limited specifically for variable higher-level taxa. Likely this leads to an incomplete understanding of the processes in general. Perhaps the most well understood of ecological concepts are those surrounding less abstract notions, like populations. It is appropriate that an examination of biological organization across different scales would begin here.

Metapopulation dynamics has been an important concept in the conservation of individual species. It stresses the interdependence of populations of a species throughout the landscape in maintaining genetic diversity and populations in environments where local populations experience frequent depletion and recolonization (Harrison 1993). Implicit in this theory is that there exist positive and negative population interactions bi-directionally across scales. For example, one interpretation of metapopulations is a core-satellite populations approach, where there exists a strong central population and several adjacent but smaller satellite populations. There is consistent exchange of material between the components, and although the satellites are individually reliant primarily on the core population, the core is dependent also on the sum contribution of satellites. The whole is dependent upon the parts and vice-versa (Primack 1993; Noss and Cooperrider 1994). Much of this thought has been untested or tested in only a few cases. The metapopulation aspect has not been abstracted to integration with concepts like communities or ecosystems.

Exploration of scalar commonality among taxa and among concepts like populations, communities, disturbance and succession has only really just begun. The strict application of individual studies to conservation, like the one reported here, is difficult because there are few bases on which to apply them to larger scales.

Regional variance of species.

The linkage of systematics and biogeography has been the forensic effort of scientists to explain spatial and temporal variance of populations. To a large degree this has focused on external morphology, with little reference to corresponding change in other organismal qualities like physiology, or behaviour. For example, it is not always the case that organisms capable of interbreeding across a large geographic range will perform the same ecological role among the intermittent systems they inhabit. Feeding preferences would need to change, for example, as might responses to disturbance, based strictly on the fact that resources and disturbances will occur differentially across large distances. There is strikingly little reference to this basic phenomenon in literature concerned with conservation and management of species. However, my study can give specific reference to several ground beetle species that have very different disturbance determinations, dependent upon where they were trapped: *Calathus advena* Lec., *Scaphinotus marginatus* Fisch., and *Pterostichus riparius* Dej., to name just a few. The later two species may be interpreted as either mature forest-dependent (Spence *et al.* 1996) or as unresponsive or even disturbance specialists! (my current work).

Part of the regional variation may be the manner in which the containing landscapes have been disturbed and thereby affected the response dynamics of inhabiting species, as discussed above in terms of metapopulation dynamics. That is, the differential responses being cumulatively observed for carabid species may be a combination of scale effects or regional variation, or of strictly one or the other. This will remain an area for future testing, and prescribing blanket prescriptions for conservation efforts will be haunted by these technicalities.

The conservation of biological diversity.

So there are large difficulties with "how" to conserve biological diversity. At the very least the problem will require a commitment to long-term research and extensive prudence in the interim use of natural resources. But why do we care? Why spend the effort to consider the fate of a few insect species? Shirking for the moment moral and aesthetic principles in conservation theory, I would point out that carabid beetles have not been recognized as "economic", like many forest pests, nor are they solely responsible for any specialized function permitting forests to continue growing. What we should be alerted by however, is the fact that such a generalist group can be the subject of concern, especially in boreal forests, which are thought to be composed of a comparatively disturbance-resilient biota. If this group can be threatened, surely many others can. For all of the taxa that have received even less attention than the understudied arthropods, the prudent approach is to expect similar, if not more dramatic, effects.

So now the issue is concerned with disturbance and the maintenance of biological diversity in a large sense. And there are many good reasons for the conservation of biological diversity. Biotic communities are being altered at an unprecedented rate (Wilson 1985), and so are the goods and services from them that have historically supported human populations. Goods include most commercial products, like timber, food, firewood, extracts, *etc* (Palmer and Synnot 1992). Services are more indirect but from a quality of life perspective, even more important. They include perennial flow of clean water, land stabilization, sequestering of atmospheric carbon, and climate regulation (Ehrlich and Ehrlich 1981).

Noss and Cooperrider (1994) point out that this utilitarian perspective of ecosystems by itself is a double-edged sword. It provides rational arguments for biological conservation that will be universally comprehensible, but may also be used as an argument for the elimination of species that cannot be demonstrated to have immediate utilitarian value.

This is contradictory to the idea that inherent qualities of an ecological system are not frivolous, or random. The diversity of an ecological system is a fundamental quality, conferring ecosystem resistance and resilience in the face of the scale and frequency of disturbances that have been responsible for the development of that system. This tenet has not been universally substantiated, and is the subject of some debate. Studies of temperate forest herbivory would indicate that for northern temperate forests and some tropical forests, managing for diversity is a dependable strategy for reducing insect outbreaks. (Schowalter 1990, 1995*a*,*b*; Schowalter *et al.* 1986). The types of diversity to

be managed for consist not only of individual arthropod species but structural diversity at stand and landscape levels, as well as physiological diversity within and among host tree species in the forest.

Site productivity is a subset of the notion of ecosystem resilience. The maintenance of goods and services will in many cases depend on maintenance of resilience. Studies which specifically examine the relationship between biological diversity and resilience or productivity are few (Franklin *et al.* 1989; Mladenoff and Pastor 1993; Noss 1993), but there are enough data to warrant the argument that this is a critical issue of exploration.

Further arguments for the conservation of biological diversity are increasingly difficult to proffer, especially in the face of the secular needs of a growing human population. Aesthetic and moral facets of biotic conservation can be traced to a common root argument: that if these pursuits are not recognized and embraced, then the quality of existence will be further degraded. Wilson (1980) argues that humans thrive on kinship, not only of our own species, but to all those around us with which we have diverse relationships. As far as we know, in all the universe, the species on this planet are our only living relatives. To ignore the beauty of life, even as we encounter it causally in day to day living, or to shirk a moral responsibility to steward things which we are easily and passively capable of destroying, would be to sacrifice a very critical element of the human experience.

Given that there could be consensus as to why we wish to conserve biological diversity, the specifics of "what?" and "how?" remain daunting. Biological diversity is defined as the organization of life at all scales (Wilson 1985). It is possible to conserve relict populations of a large numbers of species but have the genetic and structural qualities which they formerly composed, absent from the world. The consequences for the physical environment in which we live would be stupendous. So the notion of biological diversity, although most describable in terms of number of species, should not be limited to such. Abundance and associations with other species and with structural features of the landscape are important qualities that must fall under the umbrella of concern. Again, the concept of scale becomes important in conceptualizing what it is that needs conserving.

"How?" will remain the final barrier in applying the resolve of "why?" and "what?". Because certain taxa, scales and processes are inherently difficult to observe, a perfect understanding of what is idealistically defined as biological diversity is an elusive goal (but an important one in guiding effort). In the meantime, use of natural resources will need to be managed and conserved. Coarse-filter approaches seek to focus conservation on large-scale concepts like ecosystems or landscapes, assuming that this effort will be a surrogate for all other scales of biological organization occurring within them. Again this is a top-down approach, ignoring the reverse process by which the individual contributes to the whole. It must not be forgotten that understanding of large-scale biological systems is based significantly on the specifics of individual species and communities.

In order to conserve biological diversity we must be able to measure it, and this, like the "what?" and "why?", will require a certain degree of union in approach so that regional comparisons can be rigorously made. For example, Chapter 3 suggests that regional differentiation in the responses of species to disturbance is a poorly understood phenomenon. The comparison of different studies is difficult because of different approaches and lack of agreement among researches addressing fundamentally similar issues. By improving understanding of scale and its effect on biological organization, this achievement will improve the design of compensatory large-scale strategies like coarse-filter designs.

The first steps have been taken toward recognizing the importance of scale in management of natural resources and conservation of organic diversity. The foundational theory and political will seem to be in place. The ability to make correct decisions within this context will depend on the continued refining of research effort to provide comprehension of how individual management actions will precipitate effects when practised at landscape, regional and supraregional scales. The foundation for this effort will be the continued concern and compassion of people, towards themselves, and toward the living environment that sustains them.

Bibliography

BC Forest Resources Commision. 1991. *The Future of Our Forests: Executive Summary April 1991.* Prov. of BC, Victoria, BC.

BC Min. Env./Min. For. 1995. *Biodiverstiy Guidebook.* Forest Practices Code Guidebooks. Province of BC, Victoria, BC.

Bulkley Forest District. 1997. *Copper Landscape Unit: Draft Landscape Unit Objectives and Associated Strategies.* BC Ministry of Forests, Smithers, BC.

Bunnell, F. L. 1991. Biodiversity: what, where, why, and how. pp. 29-45 *in*: *Proceedings, Wildlife Forestry Symposium.* Victoria, BC, For. Can. / BC Min. For.

Ehrlich, P. R., and A. H. Ehrlich. 1981. *Extinction: The Causes and Consequences of the Disappearance of Species.* NY: Random House.

Franklin, J. F., D. A. Perry, T. D. Schowalter, M. E. Harmon, A. McKee, and T. A. Spies. 1989. Importance of ecological diversity in maintaining long-term site productivity. pp. 82-97 *in*: Perry, D. A., R. Meurisse, B. Thomas, R. Miller, J. Boyle, J. Means, C. R. Perry, and R. F. Powers, eds. *Maintaining Long-Term Productivity of Pacific Northwest Forest Ecosystems.* Portland, OR.: Timber Press.

Harrison, S. 1993. Metapopulations and Conservation. pp. 111-28 *in*: Edwards, P. J., R. M. May, and N. R. Webb, eds. *Large-Scale Ecology and Conservation Biology.* Cambridge, MA: Blackwell Science.

Hoekstra, T., T. F. H. Allen, and C. H. Flather. 1991. Implicit scaling in ecological research - on when to make studies of mice and men. *BioScience* 41 (3): 148-54.

Lovei, G. L., and K. D. Sunderland. 1996. Ecology and behavior of ground beetles. *Annu. Rev. Entomol.* 41: 231-56.

May, R. M. 1993. The effects of spatial scale on ecological questions and answers. pp. 1-18 *in*: Edwards, P. J., R. M. May, and N. R. Webb, eds. *Large-Scale Ecology and Conservation Biology.* Cambridge, MA: Blackwell Science .

Meidinger, D., and J. Pojar. 1991. *Ecosystems of British Columbia.* Special Report Series Number 6. BC Ministry of Forests, Victoria, BC.

Mladenoff, D. J., and J. Pastor. 1993. Sustainable forest ecosystems in the Northern Hardwood Conifer Forest Region: concepts and management. pp. 145-79 *in*: Olson, J. T., ed. *Defining Sustainable Forestry.* Washington, DC: Island Press.

Niemelä, J. K., and J. R. Spence. 1994. Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. *Ecography* 17: 166-75.

Noss, R. F. 1993. Sustainable forestry or sustainable forests? pp. 17-43 *in*: Olson, J. T., *Defining Sustainable Forestry.* Washington, DC: Island Press.

Noss, R. F., and A. Y. Cooperrider. 1994. *Saving Nature's Legacy - Protecting and Restoring Biodiversity.* Washington DC: Island Press.

Palmer, J., and T. J. Synnot. 1992. The management of natural forests. pp. 337-74 *in*: Sharma, N. P., ed. *Managing the World's Forests.* Dubuque, IA: Kendall/Hunt.

Pattee, H. H. 1973. *Hierarchy Theory: The Challenge of Complex Systems*. NY: Braziller.

Primack, R. B. 1993. *Essentials of Conservation Biology*. Sunderland, Massachusetts, USA: Sinauer Associates Inc.

Prov. of BC. 1993. *British Columbia Forest Practices Code: Discussion Paper.* BC Govt., Victoria, BC.

Prov. of BC. 1994. *BC Forest Practices Code: FPC Legislation Module Resource Booklet.* Prov. of BC, Victoria, BC.

Schowalter, T. D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. *For. Ecol. & Mgt.* 78: 115-25.

Schowalter, T. D. 1995. Canopy invertebrate community response to disturbance and consequences of herbivory in temperate and tropical forests. *Selbyana* 16 (1): 41-48.

Schowalter, T. D., W. W. Hargrove, and D. A. Jr. Crossley. 1986. Herbivory in forested ecosystems. *Annu. Rev. Entomol.* 31: 177-96.

Schowalter, T. 1990. Differences and consequences for insects. pp. 91-106 *in*: Students for Forestry Awareness., ed. *Forests - Wild and Managed: Differences and Consequences.* Conference Proceedings, 19-20 Jan 1990, University of British Columbia.

Spence, J. R., D. W. Langor, J. K. Niemelä, H. A. Càrcamo, and C. R. Currie. 1996. Northern forestry and carabids: the case for concern about old-growth species. *Ann. Zool. Fenn.* 33: 173-84.

Wilson, E. O. 1980. *Biophilia*. Cambridge, MA: Harvard University Press.

Wilson, E. O. 1985. The biological diversity crisis. *BioScience* 35: 700-706.

Wilson, E. O., ed. 1986. *Biodiversity*. Boston: Harvard University Press.

APPENDIX I. Site Series determinations according to Banner *et al.* (1993) for pitfall trapping sites near Smithers, BC.

	Block	Plot	Site Series	Block	Plot	Site Series	Block	Plot	Site Series
Patch Retention	A37574 Block #1	F1-1	01	A37541 Block #3	F1-1	03	A36433 Block #5	F1-1	09
		F2-1	01		F2-1	05		F2-1	03
		F3-1	03		F3-1	01		F3-1	03
		F4-1	01		F4-1	03		F4-1	03
		E1-1	01(05)		E1-1	03		E1-1	05
		E2-1	01		E2-1	05		E2-1	03
		E3-1	05(01)		E3-1	01		E3-1	03
		E4-1	01/05		E4-1	01		E4-1	03
		P1-1	01		P1-1	06 (09)*		P1-1	05
		P2-1	03		P2-1	03		P2-1	03
		P3-1	01		P3-1	05		P3-1	01
		P4-1	09		P4-1	03		P4-1	01
		P4-2	31						
		P5-1	03		O1-1	09		O1-1	05
					O2-1	05		O2-1	03
		O1-1	01		O3-1	05		O3-1	01
		O2-1	03		O4-1	03		O4-1	03
		O3-1	01						
		O4-1	09						
Clearcut	A31698 Block #2	F1-1	05(07)	A31699 Block #4	F1-1	05	A36435 Block #6	F1-1	03
		F2-1	03(02)		F2-1	05		F2-1	01
		F3-1	06		F3-1	01		F3-1	01
		F4-1	01/05		F4-1	02-03		F4-1	06
		O1-1	05(07)		O1-1	Undetermined		O1-1	03
		O2-1	03		O2-1	05		O2-1	02
		O3-1	Undetermined		O3-1	05		O3-1	05
		O4-1	03(01)		O4-1	03		O4-1	Undetermined

*Multiple site series indicates a plot in which some traps were in a considerably different regime than others of the same cluster. The use of the #(#) format indicates the determination to have been more strongly associated with the first of the two Series. The use of the # / # format indicates an equal split between two Series

APPENDIX II. Site Series descriptions associated with trap group locations near Smithers, BC

The following site series were observed to occur where traps had been (modified from Banner *et al.* 1993).

Dry series

01 BlHm-Azalea forests are widespread in the subzone most commonly on north- and east-facing upper to lower slopes where there are deep morainal or colluvial blankets. Soils are mainly coarse-textured Podzols or Brunisols. Forests are moderately productive and dominated by balsam with minor components of spruce, western hemlock and mountain hemlock. Shrub, herb and moss layers are all well developed in these stands. Black huckleberry, and a few ferns are common. Red-stemmed feathermoss and leafy liverworts dominate; other feathermosses are also common.

03 BlHm-Feathermoss is common throughout the subzone on the upper portions of long, south- and west-facing slopes that have thin veneers of colluvium and morainal till. Stands are scrubby balsam, often with some mountain hemlock, lodgepole pine or spruce. These forests are moderately stocked and have a moderate shrub layer of black huckleberry, false azalea, and conifer regeneration. Site series 03 is floristically similar to 01 forests but thinner soils, a sparse herb layer, and scrubby forest structure distinguish the 03 from the 01.

Wetter Series

05 Bl-Oakfern-Heron's bill is very common, particularly in the southern areas of the subzone. Typical landscape locations are at the lower or toe end of slopes that receive some seepage during the year. Soils are gleyed Podzols and Gray Luvisols derived from loamy-textured morainal and colluvial deposits. Balsam forests with a well-developed understorey of oval-leaved blueberry, false azalea, conifer regeneration, and oak fern are typical. An abundance of oakfern and prominence of leafy mosses distinguish 05 from 01 forests.

06 Bl-Devil's club-Lady fern site series is found mainly at lower elevations on, or at the base of, steep slopes where abundant seepage creates highly productive conditions. These sites are usually of limited extent in the subzone. Stands are composed of large, well-spaced balsam and spruce with a dense devil's club understorey. Herb species such as oak fern, foamflower, five-leaved bramble, and spiny wood fern form a lush herb layer. The dominance of devil's club and lady fern differentiates the 06 from the 05.

09 Bl-Lady fern-Horsetail is common at lower elevations in the subzone, mainly on lower slopes where wet soil conditions limit growth on these otherwise productive sites. Trees grow on elevated hummocks with wet swales dominated by horsetails and leafy mosses. Soils are Gleysols. The prominence of horsetails differentiates the 09 from all other units.